NEURAL CORRELATES OF LONG-TERM MEMORY: THE INTERPLAY BETWEEN ENCODING AND RETRIEVAL

Eva Bauch

INSTITUTE OF COGNITIVE NEUROSCIENCE
UNIVERSITY COLLEGE LONDON

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SIGNED DECLARATION

I, Eva Bauch, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

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ABSTRACT

Neural correlates of human long-term memory encoding and retrieval have been studied in relative isolation. Memory performance, however, benefits from an overlap between processes engaged at encoding and retrieval. This thesis sought to determine how encoding-retrieval overlap affects neural correlates of memory. Four studies were conducted using electrical brain activity recorded from the scalps of healthy adults. The first experiment addressed whether congruency in mode of presentation across study and test (word or picture) influences encoding-related activity. The findings showed that this was indeed the case, but only for pictures. When a picture was probed with a picture, activity over anterior scalp sites predicted encoding success. When a picture was probed with a word, encoding-related activity was instead maximal over posterior sites. The remaining experiments determined whether the amount of perceptual information contained within a picture affects memory-related activity. Study-test congruency primarily affected encoding-related activity, irrespective of the amount of information that had to be encoded. Retrieval-related activity, by contrast, was instead sensitive to the amount of information contained within a retrieval probe. Analyses in the frequency domain suggested that memory retrieval relies on the reinstatement of neural activity across study and test. Oscillatory power in the theta frequency band (4-8 Hz) over frontal scalp sites at both encoding and retrieval was specific to the encoded amount of pictorial information. Together, the data demonstrate that neural correlates of long-term memory are sensitive to the similarity between processes engaged at study and test. However, study-test overlap may not be a universal organizing principle. Effects of study-test congruency depend on the type of information contained within a study event and test probe, and the type of neural activity that is considered.

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CHAPTER 1: INTRODUCTION

My PhD research aimed to elucidate how neural correlates of episodic memory vary depending on the similarity of cognitive processes during encoding and retrieval. Episodic memory is the type of memory that is affected most by the ageing process and by neurodegenerative diseases such as Alzheimer's. It is the type of long-term memory that stores specific experiences with reference to space and time (i.e. what happened, when did it happen, what did it look like; Tulving, 1983). For instance, episodic memory allows us to remember what we had for lunch today rather than the day before. The kind of meal will be remembered via associations between different elements of this event.

Whether we will remember an event is dependent on at least two distinct processes: 1) the encoding processes engaged during the initial experience of an event and 2) the retrieval processes that allow us to call up the event into the present. Cognitive frameworks such as the transfer-appropriate processing framework highlight the importance of the interplay between encoding and retrieval processes for memory success (Roediger, 1990; for a similar framework see Tulving & Thomson, 1973). Memory retrieval benefits from an overlap between operations engaged during encoding and those during retrieval (Roediger, Gallo & Geraci, 2002). In line with this framework, neural models of episodic memory state that the likelihood of remembering an event is dependent on whether processes that were engaged during the encoding process itself are reinstated at retrieval (e.g. Alvarez & Squire, 1994; Norman & O`Reilly, 2003). These models predict that successful memory retrieval depends on the reinstatement of encoding-related cortical activity patterns during retrieval.

For more than decades, memory research in cognitive neuroscience has investigated encoding and retrieval processes and their underlying neural correlates. Although behavioural findings deliver robust evidence for the transfer-appropriate processing framework, thus far, studies into the neural bases of episodic memory have focused on either the encoding or retrieval phases of episodic memory. It is therefore largely unknown how the degree of overlap between study and test processing influences the type and amount of neural activity associated with encoding and retrieval.
Initial studies suggest that similarity between study and test processing can indeed affect neural correlates of episodic memory. For instance, a few functional magnetic resonance imaging (fMRI) studies have shown that neural activity associated with the encoding of information can be re-activated when that information needs to be retrieved (e.g. for review see Rugg, Johnson, Park, & Uncapher, 2008; Johnson, Duff, Rugg & Norman, 2009; Johnson & Rugg, 2007). Furthermore, a recent study using event-related fMRI during encoding provided evidence that neural correlates of successful encoding vary depending on how memory is later probed (Otten, 2007). However, little is known about how the neural correlates of both encoding and retrieval are affected by the congruency between study and test operations.
To gain more insights about processes supporting effective episodic memory, research on the interplay of encoding and retrieval is of great importance. Chapter 1 provides an introduction of the relevant theoretical background and the neuroscientific method that has been used throughout my PhD. The introductory Chapter closes with an outline of the research aims of my doctoral thesis. These research aims lead to the experimental Chapters 2, 3 and 4. Finally, in Chapter 5 the results are summarised and placed into context with the previous literature. Moreover, general implications and future directions are discussed.

1.1 HUMAN LONG-TERM MEMORY

The human long-term memory consists of different memory systems (Schacter & Tulving, 1997; Tulving, 1983; 1985). Non-declarative or implicit memory refers to memories for automatic or procedural skills (e.g. cognitive and motor skills such as how to read or ride a bike), the perceptual representation system (e.g. perceptual priming), classical conditioning and nonassociative learning. Non-declarative memory is based on unconscious memories and reveals improvements in task performance in the absence of explicit recollection of the information. In contrast, declarative or explicit memory refers to conscious memory representations and is divided into the semantic and episodic memory systems. Semantic memory refers to world knowledge or factual knowledge which is remembered in the absence of any recollection of personal experiences or specific details such as when the information was initially learned (e.g. London is the capital of England). In contrast, episodic memory reveals memories of our lives and personal experiences and is associated with the recollection of specific details with reference to space and time (Tulving, 1983; 1985).

Effective episodic memories are dependent on three processing stages (Gardiner, 1988; Tulving, 1985). First, the encoding stage refers to the process when experiences and incoming information are initially encountered and formed into new memory representations. The second stage refers to the consolidation of information supporting the long-term storage and retention of memory representations (Atkinson & Shiffrin, 1968; Baddley, 1997; 2001). Third, the retrieval process refers to the recovery of episodes from the past. Episodic retrieval is based on the interplay between the retrieval cue and the memory trace leading to a reconstruction of the episodic information (Tulving, 1985).

Memory performance is influenced by these three processes and by the interaction between them (Godden & Baddeley, 1975; Morris, Bransford & Franks, 1977; Tulving & Thomson, 1973). For instance, the depth or level of processing at encoding has been suggested to affect successful memory (for reviews see Craik, 2002). The impact of depth of encoding has been initially demonstrated by Craik and Lockhart (1972). In one of the encoding conditions participants had to judge whether words were presented in upper or lower case. This condition was suggested to be mainly focused on the physical attributes of the words. In a second condition, participants were focused on the phonological attributes by determining whether or

not a presented word rhymed with another word. In a third condition, deep encoding processes were emphasised, because participants had to make judgements about the meaning of the words (e.g. whether the item depicted by the word can fly). Craik and Lockhart (1972) showed that the likelihood to remember an event was highest when an event was encoded deeply with an emphasis on its semantic attributes as compared to when items were processed in terms of their phonological or physical attributes. Besides the depth of processing, memory has been demonstrated to be better when encoding emphasises associations between items in comparison when encoding was only focused on a specific item (Hunt & Einstein, 1981).

In addition to the type of encoding processes, the type of retrieval process affects memory success (e.g. Morris et al., 1977). Memory can be retrieved via different types of memory tests such as free recall, cued recall or recognition (Tulving, 1985). Free recall refers to the retrieval of initially encountered information in absence of external cues. In a cued recall test, cues are presented that may be related to the target item in terms of its semantic, phonological or physical attributes to support the recovery of the target item. In a recognition memory test, all initially studied items (old) are presented again intermixed with unstudied (new) items. Participants need to differentiate whether the item is old or new. Free recall tests are thought to tap into episodic memory retrieval processes and refer to stronger memories, because these tests are less vulnerable to contaminations by lucky guesses (Tulving, 1974).

In terms of processes that support recognition memory, there is an ongoing question of whether recognition memory is based on one type of mnemonic process (Squire, Wixted & Clark, 2007) or whether it is supported by at least two distinct processes (Mandler, 1980). On the one hand, single process models state that recognition memory is based on one memory type that can vary in terms of its memory strength (Dunn, 2004; McClelland & Chappell, 1998; Squire et al., 2007). In contrast, dual process accounts state that recognition memory is based on two functionally distinct processes (for review see Eichenbaum, Yonelinas & Ranganath, 2007; Greve, Donaldson, & van Rossum, 2010; Rugg & Yonelinas, 2003). According to dual process models, information can be remembered based on recollection and familiarity (for review see Yonelinas, 2002). Recollection refers to the retrieval of contextual information of the episode. In contrast, familiarity is based on simple recognition in absence of any contextual information (Tulving, 1985). A typical example for recognition memory based on familiarity is the phenomenon of simply

recognising and knowing a person without recollecting the persons name or other specific contextual details (Mandler, 1980). Tulving et al. proposed that recollection and familiarity rely on independent memory systems: episodic and semantic memory systems (Yonelinas, 2002). Neuroimaging studies show consistent support that recollection and familiarity refer to two qualitative distinct processes, because both were associated with different brain regions (e.g. Davachi, Mitchell & Wagner, 2003; Rugg, Otten, Rugg, 2002; Rugg & Yonelinas, 2003; Vilberg & Rugg, 2008; Yonelinas, Otten, Shaw & Rugg, 2005; for caveat see Squire et al., 2007).

Therefore, a simple old/new recognition test that differentiates only between studied (old) and unstudied (new) responses may not be sufficient to tap into episodic memories, because recognition judgements are possibly confounded by memories based on recollection and familiarity. There are various approaches to dissociate between recognition memory based on recollection and familiarity (e.g. Jacoby et al., 1993; Yonelinas, 2002). One well-established method is the remember/ know (R/ K) recognition test that is based on the subjective judgements of the participants (Gardiner, 1988; Gardiner & Richardson-Klavehn, 2000; Tulving, 1985). At test, participants need to differentiate between 'remember' responses (i.e. they have seen the item at study and can remember contextual details about the episode), 'know' responses (i.e. a general feeling of knowing the item without any recollection of specific details) and 'new' responses (i.e. unstudied item). Remember responses are suggested to reflect mainly recollection processes and know responses familiarity-based recognition memories (Yonelinas, 2002; Yonelinas & Jacoby, 1995). Various experimental manipulations and neuroimaging findings provide support that remember and know judgements are associated with distinct processes (Diana, Yonelinas & Ranganath, 2007; Rugg & Curran, 2007; for caveats see Rotello, MacMillan & Reeder, 20045; Wais, Mickes & Wixted, 2008). For instance, depth of encoding has been shown to selectively affect remember responses (e.g. Gregg & Gardiner, 1994; Rajaram, 1993). Although the R/K procedure has been commonly used to tap into recollection-and familiarity-related processes, there are a few issues that need to be considered. For instance, remember and know responses may be confounded by different confidence levels. Remember responses may be based on confident judgements, whereas know responses are given when participants are unconfident about whether or not the item was studied before or when they guessed (Geraci, McCabe, & Guillory, 2009; McCabe & Geraci, 2009; Yonelinas, 2002).

Therefore, instead of tapping into distinct types of memories, only different levels of memory strength may be tested.

Modifications of the R/K procedure have been introduced to dissociate between the type of recognition memory and the level of confidence (Voss & Paller, 2009; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). For instance, instead of one of three recognition judgement participants are asked to give one of five recognition responses. If participants are confident that they have seen the item at study and can remember something specific about it, they need to press the 'remember' response (recollection-based judgement). If they are only confident that they have seen the item before in the absence of any specific details, they give the 'confident old' response (familiarity-based judgement). If participants are unconfident whether they have seen the item before, they press the 'unconfident old' response. Moreover, if they are unconfident whether they have not seen the item before, they need to respond with 'unconfident new' and if they are sure about whether the item is new , they press 'confident new'. Crucially, 'remember' and 'confident old' responses dissociate memories based on recollection and familiarity, but rely both on high confident judgements. A simplified version of this R/K procedure is based on only three response options. Participants need to differentiate between 'remember' (confident recollection-based memories) and 'confident old' (confident familiarity-based memories) and 'new' responses that consist of confident new and unconfident responses. Neuroimaging studies show support that the modified R/K versions may be able to dissociate between brain activity related to recollection-based memories and familiarity-based memories and the confidence level (Voss & Paller, 2009; Woodruff et al., 2006, Yonelinas et al., 2005; Yu & Rugg, 2010). In all of my PhD experiments except for one study I applied the modified three-way R/K procedure to dissociate between confident recollection-based memories and familiarity-based memories.

1.2 TRANSFER-APPROPRIATE PROCESSING FRAMEWORK AND BEHAVIOURAL SUPPORT

Memory success is not only dependent of the type of encoding process and type of retrieval process, but also on the interplay between processes at encoding and retrieval (Kolers & Roediger, 1984; Roediger 1990, Rugg, Johnson, Park & Uncapher, 2008). Behavioral studies have found evidence supporting the transfer-appropriate processing principle (e.g. Blaxton, 1989; Dewhurst & Knott, 2010; Hyde & Jenkins, 1969; Jacoby, 1983; Leboe, Whittlesea & Milliken, 2005; Morris et al., 1977; Mulligan, Besken & Peterson, 2010). The transfer-appropriate processing principle originally arose from studies that aimed to explain why memory success varied as a function of the type memory test (Morris et al., 1977). For instance, Jacoby (1983) demonstrated that deep encoding processes do not always lead to better memory performance under all circumstances, but that the similarity of encoding and retrieval operations also determines later memory success. At study, target words were either read or generated from words that were semantic related to the target words. At test, the studied words were either presented in a standard recognition test or in a perceptual identification test. In the latter test, participants were asked to identify target words that were briefly (35 ms) presented. While words that were read at encoding led to better memory performance in the perceptual identification task, words that were initially generated were better remembered in the standard recognition task. Jacoby (1983) proposed that words have to be perceptually analysed in order to be recognized in the perceptual identification task. Therefore memory was best for those words that were read at encoding, because this encoding process emphasised the perceptual features of words. On the other hand, the recognition test was suggested to be conceptually-driven (i.e. semantic processes are emphasised). Therefore, words were best remembered when they were initially generated, because this encoding process also emphasised conceptual processes.

Besides interpreting the data in terms of an appropriate transfer of processes between encoding and retrieval, Tulving's memory systems framework (1983) raised the possibility that the performance differences as a function of the type of memory test may be related to the fact that the memory tests tap into two different types of memory systems, episodic and semantic memory or explicit and implicit memory (Tulving, 1983). Blaxton (1989) addressed this possibility by manipulating the degree of encoding-retrieval overlap and the type of memory test within one experiment. At study, words were again read or generated. Five different memory tests were used. Some of these tests relied on semantic memories and the others on episodic memories. Moreover, the tests emphasised either conceptual processes or perceptual processes. For instance, a general knowledge test was assumed to rely on semantic memory and conceptual processes. In contrast, a word fragment completion test relied on semantic memory, but emphasised perceptual processes, because the completion of the fragments required the analysis of physical features of the word. Blaxton (1989) demonstrated that memory for items that were read (i.e. perceptually- processed) during a study phase was best in a word fragment completion test. By contrast, words generated during a semantic processing task were best remembered when the test phase focused on semantic information. Together the findings provided good support for the transfer appropriate principle account. In accordance with Blaxton's findings, Morris et al (1977) reported that memory retrieval does not always benefit from deep encoding processes. Memory performance was better for phonologically encoded information (i.e. rhyming task) rather than semantically encoded items when old items were tested in a phonological task (i.e. rhyming recognition task).

Another approach to vary the different types of operations (i.e. conceptual and perceptual processes) and their similarity between study and test is to manipulate the physical similarity between study and test material in recognition tests. A number of studies have demonstrated that the study-test congruency of the presentation mode benefits memory retrieval. Recognition accuracy tends to be better when test items are presented in the same format as during study (i.e. word-word or picture-picture) than when it is shown in the alternative format at test (i.e. word-picture, picture-word) (e.g. Ally & Budson, 2007; Ecker, Zimmer, & Groh-Bordin, 2007; Gardiner, Gregg & Karayianni, 2006; Groh-Bordin., Zimmer & Ecker, 2006; Mintzer & Snodgrass, 1999; Rajaram, 1993; Schloerscheidt & Rugg, 2004; Stenberg, Radeborg & Hedman, 1995; Weldon & Roediger, 1987). Studies which investigated how this manipulation influences recollection and familiarity show mixed results (Jacoby, 1996; Rajaram, 1993; Schloerscheid & Rugg, 2004). The findings are variable in terms of whether effects of study-test congruency are specific to recollection (Hirshman, Passanante& Arndt., 1999; Park & Rugg, 2008; Reder, Donavos & Erickson, 2002) or also affect familiarity (Reder et al., 2002; Rajaram & Geraci, 2000).

While there is evidence on the behavioural level, support on a neural level for encoding-retrieval overlap still needs to be provided. A summary of imaging findings in the encoding and retrieval literature that are relevant to my research are provided along this introduction. But, beforehand the neuroscientific method that has been used throughout my thesis is described.

1.3 ELECTROENCEPHALOGRAPHY: INVESTIGATING THE RELATIONSHIP BETWEEN THE BRAIN AND COGNITIVE PROCESSES

Throughout my PhD the electroencephalogram (EEG) was used as a neuroscientific method to investigate neural correlates of long-term memory. The EEG is one of the most established neuroscientific methods to examine non-invasively the relationship between cognitive functions and brain activity. The EEG reads continuous electrical brain activity from the scalp surface. The electrical brain activity is obtained via an electrode cap that is placed on the head of the participants during the recording. The EEG measures synchronous post-synaptic activity of neuronal populations that are perpendicularly oriented to the scalp surface (Luck, 2005). Pyramidal cells are suggested to produce the EEG activity, because they are oriented perpendicularly and fire synchronously (Luck, 2005). The individual neuronal activities that occur simultaneously sum up and create an electrical field that is evident at the scalp surface (Rugg & Coles, 1995). However, if the neuronal activity is not synchronised or if the activity is elicited by neuronal populations that are not spatially aligned, the neuronal activity would not be evident in the EEG (Roach & Mathalon, 2008). The temporal resolution of EEG is higher than other imaging techniques such as fMRI or positron emission tomography (PET) that measure hemodynamic responses. Because changes in electrical brain activity are measured in the range of milliseconds (Otten & Rugg, 2004), EEG is preferably used to investigate quick cognitive processes. However, in contrast to hemodynamic measures such as fMRI or PET, the neuronal generators of electrical brain activity are difficult to define (Luck, 2005; Nunez, 1995). The EEG data are measured from the scalp surface after the brain activity is filtered through other brain structures and the cranial bones (i.e. volume conduction; Luck, 2005). The difficulty to define the location of the neuronal activities based on the voltage distribution across the scalp is called the inverse problem. A specific voltage distribution is not unique to one set of neuronal activities (Luck, 2005). Therefore, a direct localisation within the brain is very difficult.

There are two well-established approaches to examine the relationship between electrical brain activity and associated cognitive functions; event-related potential and time-frequency approaches.

1.3.1 EVENT-RELATED POTENTIALS

Event-related potentials (ERPs) are electrical brain signals that are evident in the EEG when sensory or cognitive information is processed (Rugg & Coles, 1995). The majority of the recorded EEG contains signals that are unrelated to the processes that are associated with the experimental events. This activity is also called background activity that adds noise to the data. ERPs usually have smaller amplitudes (1-30 μV) than the background EEG. The ERP refers to the average of those EEG signals that are related to the presented stimulus. Crucially, this average approach is based on the assumption that repetitions of the same stimulus elicit similar signals and that the background noise is randomly distributed across the experimental events. Thus, the ERP approach makes it possible to extract the event-related EEG signal from the background noise by averaging those EEG signals that are time-locked to the event. The signal-to-noise ratio improves with the number of trials that are included in the average, because random background EEG will be cancelled out and, in turn, the event-related brain activity will be cleaner (Luck, 2005).

The outcome of the averaging process is a series of positive and negative voltage fluctuations that can vary in various kinds of dimensions: time, polarity, amplitude and the distribution across the scalp (Rugg & Coles, 1995). These characteristics need to be replicated across various individuals to assume a reliable ERP effect. The specific dimensions can vary across experimental conditions (e.g. remembered versus forgotten items) (Otten & Rugg, 2004). For instance, differences in the onset of ERPs across experimental conditions indicate that one underlying process emerges later than the other. A difference in amplitude across conditions reflects the different degree of involvement of the same cognitive processes. In contrast, differences in the scalp distribution or polarity between the ERPs indicate the engagement of qualitatively different kinds of cognitive processes (Otten & Rugg, 2004). However, due to the low spatial resolution of EEG it is very difficult to localise a precise source or neuronal generators of the ERP effects.

On the other hand, non-significant differences between two conditions do not have to refer necessarily to the same process. One reason for the absence of a difference may be related to a low statistical power to detect differences. Moreover, the ERP effects may involve different processes, but the amplitude might be too small or the spatial alignment of the neuronal populations may not be optimal to be detected on the scalp (Otten & Rugg, 2004).

1.3.2 TIME-FREQUENCY ANALYSIS

The interest in investigating oscillatory activity and its relationship to associated cognitive functions became increasingly popular in the 1990s with advanced recording equipment, signal analysis techniques and computer hardware and software. Oscillatory EEG responses are rhythmic and repetitive EEG fluctuations that are suggested to play an important role for the dynamic communication between functional brain networks and the binding of information that is processed in different brain areas (for review see Bastiaansen, Mazaheri, & Jensen, 2008; Rosch & Mathalon, 2008). EEG oscillations are characterised by power and phase (Roach & Mathalon, 2008). Oscillatory power refers to increases or decreases in amplitude of EEG oscillations and reflects changes in neural synchronization or desynchronisation (Roach & Mathalon, 2008). Oscillatory phase refers to a specific point in time of the oscillation (i.e. slope). The event-related oscillatory EEG signals can be phase-locked to the event (i.e. evoked) or the phase can vary across trials (i.e. induced) (Bastiaansen et al., 2008). An ERP approach may not be an optimal analysis method in this context because the average of EEG signals across trials would diminish the informative non-phase locked oscillatory EEG signals. Instead, time-frequency approaches are applied, because they decompose oscillatory activity that is phase locked and not phase-locked to the event (Bastiaansen et al., 2008). Crucially, event-related changes in power or phase of oscillations are derived for each single trial. Besides induced and evoked activity EEG oscillations also contain spontaneous fluctuations that are unrelated to the experimental event. This noise can be cancelled out by averaging the time-frequency information across a number of experimental events (Herrmann, Grigutsch, & Busch 2005).

There are various time-frequency analysis approaches (e.g. Klimesch, Russegger, Doppelmayr & Pachinger, 1998; Mitra & Pesaran, 1999). Wavelet analyses represent one of the most established analysis methods, because this approach provides a good resolution in both the temporal and frequency domain (van Vugt, Sederberg & Kahana, 2008). The event-related changes of power and phase of oscillations can be examined at specific frequencies such as delta (1-3 Hz), theta (4-8 Hz), alpha (9-12 Hz), beta (13-30 Hz), and gamma (>30 Hz) (Roach & Mathalon, 2008). My PhD research focused on oscillatory power changes in the theta frequency range (4-8 Hz), because previous research showed consistent evidence that theta power plays an important role in episodic encoding and retrieval processes (for reviews see Düzel, Penny & Burgess, 2010; Klimesch, Freunberger, Sauseng & Gruber, 2008; Nyhus & Curran, 2010).

1.4 MEASURING THE NEURAL CORRELATES OF SUCCESSFUL ENCODING: SUBSEQUENT MEMORY EFFECT

A common procedure for investigating the neural correlates of episodic encoding is the 'subsequent memory paradigm' (Paller, Kutas & Mayes, 1987). This procedure has been used with different measures of neural activity, including EEG (Otten & Rugg, 2001a; Paller et al, 1987; Sanquist, Rohrbaugh, Syndulko & Lindsley, 1980; Weyerts, Tendolkar, Smid and Heinze, 1997); fMRI (Brewer, Zhao, Desmond, Glover & Gabrieli, 1998; Wagner et al., 1998; Otten, Henson & Rugg, 2001; Otten & Rugg, 2001b); magnetencephalography (MEG) (Takashima, Jensen, Oostenveld, Maris, van de Coevering & Fernandez, 2006) and intracranial recordings (Fell et al., 2001).

In this paradigm, subjects are shown a series of items which they either encode incidentally or intentionally while their brain activity is recorded. In an incidental encoding paradigm, participants encode items in a particular task (e.g. size judgement task) without knowing that their memory will be later tested. In contrast, in an intentional encoding paradigm participants are informed that their memory will later be tested and that they need to memorise the items in a particular way. After a delay, their memory is tested for the studied items. Neural activity evoked by each item during the study phase is categorized based on their memory performance in the subsequent memory test; according to whether the item was later remembered or

forgotten (see Figure 1). The difference between the brain activity of later remembered and forgotten items is called an 'subsequent-memory effect' and is thought to be an index of successful memory formation (for review see Paller & Wagner, 2002). In sum, using the subsequent memory paradigm enables to identify encoding-related activity that predicts later memory success or failure.

Although the subsequent memory paradigm is a well established approach to isolate encoding-related activity from other cognitive processes, there are a few issues that need to be considered. For instance, the subsequent memory effect may not have to reflect necessarily pure memory encoding success, but may be also modulated by attentional processes; whether an item was attended or not. Thus, the difference between later remembered and forgotten items may reflect rather attentional-related brain activity instead of activity related to memory formation. Therefore, behavioral measurements such as reaction time (RT) or task accuracy need to be considered to dissociate between encoding-related and attentional-related processes. Trials that are based on too early or too late or incorrect responses or misses at encoding need to be excluded from the analyses. Furthermore, analyses of the RT during encoding according to whether the item was subsequently remembered or forgotten are used to clarify whether attentional processes have an influence on the subsequent memory effect (Rugg et al., 2002; Wagner, Koutstaal & Schacter., 1999).

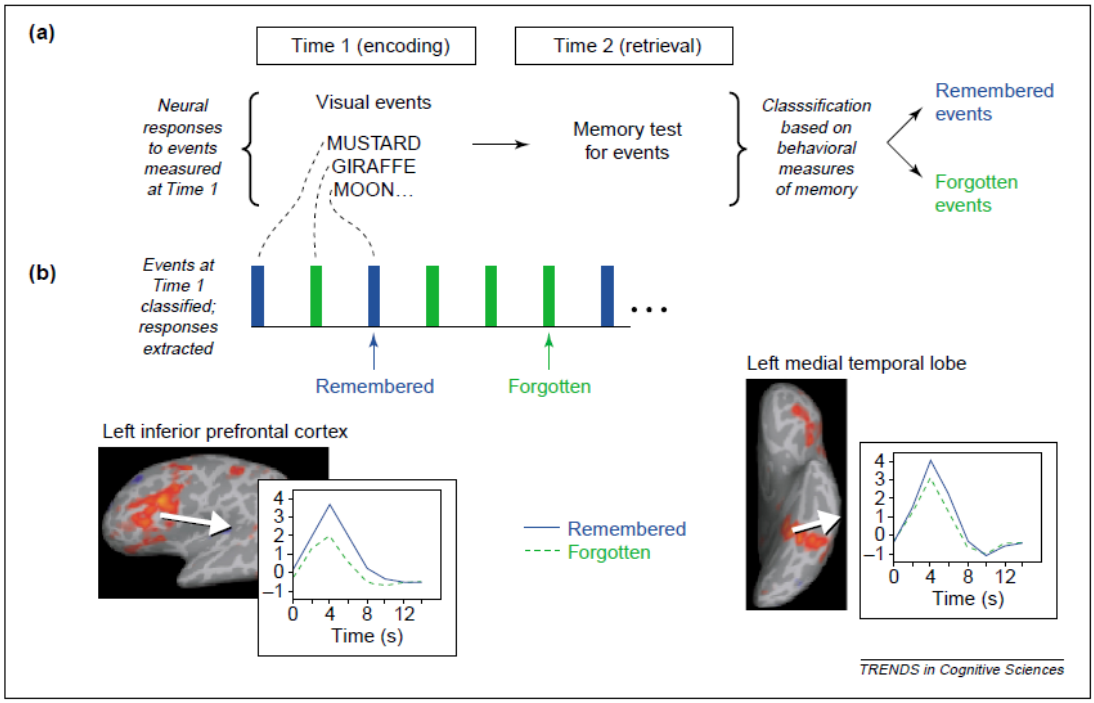

Figure 1. The subsequent memory paradigm. (a) Neural responses acquired during event processing (in this example, visual word presentations). Subsequently, memory is probed and events are classified. (b) Neural responses are analyzed based on subsequent memory, revealing neural correlates of encoding in various brain regions. Graphs (redrawn from Ref. 8) show that remembered events (blue) elicited greater responses than forgotten events (green). (Figure and legend taken from Paller & Wagner, 2002).

1.5 NEURAL CORRELATES OF ENCODING

1.5.1 NEURAL CORRELATES OF ENCODING – INFLUENCE OF TYPE OF ENCODING

In this section, electrophysiological and fMRI findings investigating encoding-related brain activity with the subsequent memory paradigm are presented. In accordance with the transfer-appropriate principle that memory representations for the same event can differ depending on what type of attributes were emphasized during the encoding process (e.g. perceptual or semantic features), imaging findings suggest that there is no single neural system supporting successful memory formation (Fletcher, Stephenson, Carpenter, Donovan & Bullmore, 2003; Wagner et al., 1998). Encoding-related activity seems to be a 'byproduct' of the processing of the event during the study phase itself (cf. Otten & Rugg, 2001b, pp 1159; Harvey, Fossati & Lepage, 2007; Otten, Henson & Rugg, 2002, Mitchell, Macrae & Banaji, 2004). Consistent with this assumption, ERP and fMRI findings have demonstrated task-specific activity related to successful encoding. For instance, in Otten and Rugg (2001b) series of words were either encoded semantically or phonologically. The brain regions related to encoding success differed according to the type of study task. While subsequent memory effects associated with semantic processing were pronounced over medial and left inferior frontal cortex, subsequent memory effects related to phonological judgments were shown in posterior cortical regions. These regions that were specific to the particular study task overlapped partly with brain areas that were engaged during the processing of each study task irrespective of later memory performance (see also Wagner et al., 1998). However, there are also a few studies that show that non-semantic encoding tasks overlapped partly with regions that were related to semantic processing (Baker, Sanders, Maccotta & Buckner, 2001; Otten et al., 2001).

In addition to task-sensitive encoding-related effects, fMRI findings have demonstrated material-sensitivity of subsequent memory effects (Brewer et al., 1998; Golby et al., 2001; Otten, Sveen& Quaale, 2007; Paller & Wagner, 2002; Uncapher & Rugg, 2009). Encoding-related activity for salient stimuli such as emotional stimuli or stimuli related to reward has been associated with distinct brain regions. For instance, activation in the amygdala is correlated with later memory success (Dolcos, LaBar & Cabeza, 2004a,b). Moreover, activity in dopaminergic midbrain regions associated with reward processing such as the nucleus accumbens and ventral tegmental area predicted later memory success (Wittmann, Schott, Guderian, Frey, Heinze & Düzel, 2005; Wittmann, Schlitz, Boehler & Düzel, 2008).

In addition to content and material-specific encoding-related regions the prefrontal cortex (PFC) and medial temporal lobe (MTL) have been suggested to play an important role for episodic memory formation irrespective of the content or type of stimulus material (Blumenfeld & Ranganath, 2007; Davachi, 2006). Distinct regions within the PFC are thought to reflect different kind of control processes supporting memory encoding. While the ventrolateral regions have been associated with control processes supporting the selection of goal-directed information, the dorsolateral regions have been linked to organising the different elements of the incoming information (Blumenfeld & Ranganath, 2007; Fletcher & Henson, 2001). The hippocampus has been suggested to play a crucial role in binding the representations from different cortical activity patterns to a detailed episodic trace which in turn supports the successful retrieval of contextual details (Davachi, 2006; Staresina & Davachi, 2008).

EEG studies using the subsequent memory paradigm, consistently report more positive-going ERPs for later remembered relative to later forgotten items between around 300 and 800 ms after item onset (for reviews see Friedman & Johnson, 2000; Paller & Wagner, 2002). In accordance with fMRI findings, ERP studies report differences in subsequent memory effects in terms of extent (amplitude), timing and distribution over the scalp according to the kind of encoding task. The subsequent memory effect is usually maximal over frontal or frontocentral electrode sites in semantic or elaborative encoding tasks (Friedman & Johnson, 2000; Otten & Rugg, 2001; Otten et al., 2007; Paller & Wagner, 2002; Wagner et al., 1999). In contrast, study tasks emphasising non-semantic processing or specific attributes of an item elicited more parietally distributed subsequent memory effects (Fabiani, Karis & Donchin, 1986; Karis, Fabiani & Donchin, 1984; Otten & Donchin, 2000).

There are only a few ERP studies comparing subsequent memory effects according to the stimulus material. For example, Sommer, Kosmos, and Schweineberger (1997) showed that subsequent memory effects elicited by unfamiliar faces differed in their scalp distribution from the effects evoked by words. The effect for words was more frontally distributed and slightly larger over the right hemisphere. Faces elicited a more symmetric and centrally distributed subsequent memory effect (see also Yovel & Paller, 2004). ERP findings demonstrated a subsequent memory effect with a parietal distribution for line drawings (Friedman & Sutton, 1987) and a more right pronounced subsequent memory effect for objects (Duarte, Ranganath, Winward, Hayward, & Knight, 2004). In contrast, studies using abstract or symbolic stimuli did not report a subsequent memory modulation (Musen & Triesman, 1990; Van Petten & Senkor, 1996).

Brain oscillations in the theta frequency range (4-8 Hz) are thought to play an important role in episodic memory encoding and retrieval (for review see Düzel et al., 2010; Nyhus & Curran, 2010). Theta oscillations have been suggested to support the dynamic communications between memory-related brain networks. Studies using the subsequent memory paradigm reported consistently a relative increase in theta power for later remembered relative to forgotten items (for reviews see Düzel et al., 2010; Nyhus & Curran, 2010; other findings (Fell et al., 2011; Guderian, Schott, Richardson-Klavehn & Düzel, 2009). In accordance with the outlined fMRI findings, intracranial EEG studies demonstrated that activity in the theta frequency band (4-8 Hz) is associated with successful memory formation within the MTL and the PFC (Fell et al., 2001; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Sederberg et al., 2007). Little is known about whether encoding-related theta power effects vary with the type of stimulus material or encoding task. The majority of the previous studies used words as stimulus material. A lot of these studies reported frontal encoding-related theta power effects (Hanslmayr, Spitzer & Bäuml, 2008; Moelle, Marshall, Fehm & Born, 2002; Sederberg et al., 2003; Summerfield & Mangels, 2005). In contrast, a couple of studies demonstrated that pictures (Osipova, Takashima, Oostenveld, Fernandez, Maris & Jensen, 2006) and faces (Moelle et al., 2002) elicited right parietal encoding-related theta power effects. Although the type of stimulus material has not been manipulated within one experiment, the topographical differences suggest material-specific effects of the encoding-related theta power.

In sum, neuroimaging studies demonstrate that there is not one unique encoding-related network, but encoding-related brain activity varies as a function of the type of encoding process and stimulus material.

1.5.2 NEURAL CORRELATES OF ENCODING – INFLUENCE OF TYPE OF RETRIEVAL CUE

Considering the transfer-appropriate processing framework, it has been predicted that the neural correlates of encoding differ depending on the type of retrieval process (Rugg et al., 2008). It is largely unknown how neural correlates of memory formation depend on how memory for an event is later probed. There are only few fMRI findings which add insights into how neural correlates of memory formation are influenced by retrieval processes.

For instance, neuroimaging studies have shown that the type of memory judgment can affect encoding-related activity. Encoding-related activity have been shown to vary according to whether recognition judgements are based on recollection or familiarity (Davachi et al., 2003; Ranganath, Yonelinas, Cohen, Dy, Tom, & D'Esposito, 2004) or on explicit or implicit memory (Schott, Richardson-Klavehn, Heinze, & Düzel, 2002; Schott, Richardson-Klavehn, Henson, Becker, Heinze & Düzel., 2006). ERP studies have shown that subsequent memory effects based on remember judgements lead to larger subsequent memory effects than for know responses (Voss & Paller, 2009; Yovel & Paller, 2004). fMRI findings demonstrated activation of distinct brain regions as a function of whether memory was based on recollection or familiarity, whereas encoding-related effects based on recollection were found in the hippocampus and parahippocampal regions, familiarity-related effects were specific to the perirhinal and entorhinal areas (Davachi et al., 2003; Ranganath et al., 2004; for other findings see Brewer et al., 1998).

Consistent with the transfer-appropriate framework, a recent event-related fMRI study (Otten, 2007) demonstrated that neural correlates of successful encoding vary depending on how memory is later probed. In the study phase, visual words were presented and incidentally encoded in a size judgement task. At retrieval, stimulus attributes of the studied items were varied (i.e. presenting a spoken word-cue or picture-cue). Different brain regions related to successful encoding were activated according to whether the item was later cued by a word or a picture. During a later recognition memory test, successfully-encoded visual words that were cued with a spoken word elicited activity in left fusiform gyrus, right frontal and occipital cortex at study. By contrast, successfully-encoded visual word later cued with a picture showed activity in the left superior temporal gyrus, left superior frontal gyrus and right lateral

parietal cortex at study. Her findings suggest that the neural correlates of encoding seem to be a subset of all encoding-related activity, namely those that are used to retrieve an item later on.

In accordance with these findings, a recent fMRI study showed that distinct neural brain regions predict later memory success depending on the type of memory test (Wimber, Heinze & Richardson-Klavehn, 2010). Participants intentionally encoded words in a syllable counting task. At test, the words were only briefly presented (between 33 and 66 ms) in a combined perceptual identification task and recognition test. Words that were later only identified in the perceptual identification task were associated with increased activity in ventral posterior parietal and dorsolateral prefrontal cortex. In contrast, activation in ventrolateral prefrontal and dorsal posterior parietal cortex predicted later successful recognition memory. These findings are in line with the transfer-appropriate processing and show that encoding-related activity differs depending on the type of processes that are emphasised at test.

Further support is provided by Park and Rugg (2008) who addressed the question of whether encoding-related brain activity differs according to whether retrieval cues are congruent or incongruent in its material to those during study. At study, intermixed words and pictures were presented in a size judgement task. At retrieval, half of the studied items were shown in the same format as during study and half in the alternative format. Contrasts at study were conducted for activity related to later successfully recognised items in response to study-test congruence versus incongruence. In congruent conditions for both stimulus materials (i.e. words-words; picture-picture), brain activity was greater in regions that were activated by the online processing of the particular stimulus material. For example, subsequently recognised words that were later cued in the same format elicited greater activity in left superior temporal cortex than words later tested with pictures, suggesting that words in the congruent condition were processed in a more 'word-like manner' than words that were later tested in the alternative format (Park & Rugg, 2008).

In the same vein, Bridger and Wilding (2010) investigated the influence of retrieval requirements on the electrophysiological correlates of encoding. Participants encoded words in two types of incidental encoding tasks (i.e. pleasantness and drawing tasks). The words were either presented on the left or right of fixation. At test, participants were asked to either recollect the screen location or the type of encoding task that was associated with the target word. Encoding-related brain activity differed qualitatively as a function of whether the location or the type of encoding tasks had to be recollected. It was suggested that these encoding effects reflect most likely the encoding processes that are necessary to retrieve the representation. In sum, neural correlates of successful encoding appear to differ qualitatively according to encoding processes (i.e. type of encoding task and stimulus material) and on the type of retrieval cue.

1.6 NEURAL CORRELATES OF RETRIEVAL

1.6.1 NEURAL CORRELATES OF RECOGNITION MEMORY

Several different types of processes thought to be engaged when trying to retrieve information from episodic memory. Using retrieval cues accurately to recollect information from episodic memory seems to depend on an appropriate cognitive state that is maintained during the episodic retrieval phase (retrieval mode, Tulving, 1983; for review see Rugg & Wilding, 2000). Neuroimaging studies usually investigate the neural correlates of retrieval mode by comparing brain activity related to an episodic memory test relative to activity evoked by non-episodic memory tests (e.g. semantic memory test; Düzel, Cabeza, Scheich, Picton & Tulvin, 1999; Herron & Wilding, 2004).

Another retrieval process refers to the adoption of certain 'retrieval orientations' that differ according to the specific episodic retrieval requirements (e.g. words versus pictures; e.g. Hornberger, Morcom & Rugg, 2004). ERP studies consistently report that identical retrieval cues can be processed differently depending on which kind of memory representation is attempted to be retrieved (e.g. Benoit, Werkle-Bergner, Mecklinger & Kray, 2009; Hornberger et al., 2004; Robb & Rugg, 2002; Werkele-Bergner, Mecklinger, Kray, Meyer & Düzel, 2006). The neural correlates of retrieval orientations are usually investigated by contrasting activity elicited by unstudied (i.e. new) items of different retrieval tasks in order to reduce the confounding influence of activity related to retrieval success (Rugg & Wilding, 2000).

Finally, retrieval success refers to the successful recovery of the episode that is triggered by a specific retrieval cue. A common way to investigate the neural correlates of retrieval success is to contrast the brain activity evoked by correctly classified old (i.e. studied) items with the brain activity elicited by correctly classified new (i.e. unstudied) items. This difference is called an old/new effect and is thought to be an index of successful memory retrieval (for review see Friedman & Johnson, 2000). A number of ERP studies suggest the existence of several old/new effects that are dissociable from each other on the basis of their timing and scalp distribution. One robust ERP effect is the left parietal old/new effect (for reviews see Friedman & Johnson, 2000; Rugg & Curran, 2007; Rugg & Yonelinas, 2003). ERPs corresponding to old responses elicit more positive-going ERPs than those evoked by new items. This old/new effect is usually pronounced at left parietal scalp electrodes and occurs approximately between 500 and 800 ms post stimulus. The left parietal effect is thought to be an index of recollection because ERP findings show that its amplitude varies according to factors that are suggested to selectively influence recollection: depth of encoding (Rugg, Walla, Schloerscheidt, Fletcher, Frith & Dolan, 1998), correct source judgement of contextual details (Donaldson & Rugg, 1999; Wilding & Rugg, 1996) and remember judgement relative to know responses (Düzel et al., 1997; Düzel, Vargha-Khadem, Heine & Mushkin, 2001). Although the neural generators of ERP effects are difficult to determine (Nunez, 1997), the left-parietal old/new effect has been associated with the left parietal cortex and in particular with the left inferior parietal cortex (Rugg et al., 2002; Vilberg & Rugg, 2009). These assumptions are based on the demonstration that both the left-parietal ERP effect and the inferior parietal cortex seem to be more generic indices of recollection, regardless of the type

of stimulus material (Curran & Dien, 2003; Schloerscheidt & Rugg, 1997; Johnson & Rugg, 2007; for review see Rugg & Curran, 2007; Vilberg & Rugg, 2008). Furthermore, recently ERP and fMRI studies have demonstrated that the left-parietal effect and activation in the parietal cortex both vary with the amount of recollected information (Vilberg & Rugg, 2008, 2009; Rugg, Cox, Doyle & Wells, 1995; Vilberg, Moosavi & Rugg, 2006; Wilding, 2000).

Despite the empirical evidence that the left-parietal effect reflects recollection, the precise functional significance is still unclear (for review see Wagner, Shannon, Kahn & Buckner, 2005). On the one hand, it has been suggested that the effect reflects processes supporting the maintenance of the episodic information (Vilberg & Rugg, 2008, 2009; Wilding & Rugg, 1996). On the other hand, it has been proposed that the effect refers to attentional processes to the recollected information (Vilberg et al., 2006; Wagner et al., 2005). Studies that demonstrated that the parietal activity increases with the amount of retrieved information have been taken as support for the former hypothesis (Vilberg & Rugg, 2008, 2009). For instance, Vilberg et al. (2006) presented picture pairs during encoding. At test, only one picture of the pair was shown in a modified R/K paradigm. Participants had to judge whether they could 'remember the corresponding paired associate', whether they could instead 'remember any other specific details' of the episode instead, whether they just 'knew' that the item was studied or whether the item was 'new'. The authors suggested that the successful recollection of the paired associate would be associated with more recollected information than the recollection of other specific information of the episode. Vilberg et al. (2006) demonstrated that the left-parietal old/new effect was as expected greater in amplitude for the recollection of the pair associates (i.e. recollection of more episodic information). Those findings were thought to suggest that the left-parietal effect supports the representation of the recollected information (see also Vilberg & Rugg, 2009). More specifically Vilberg and Rugg (2008) proposed that the inferior parietal cortex is part of the brain networks that are associated with attentional processes to support the maintenance of episodic information within the working memory (Baddeley, 2000).

In contrast to the recollection-related old/new effect, an ERP old-new effect with a time course of approximately 300 and 500 ms post stimulus and a midfrontal scalp distribution has been consistently associated with familiarity-based recognition (for review see Rugg & Curran, 2007; Curran, 2000; Curran & Cleary, 2003; Woodruff et al., 2006; for different a view see e.g. Tsivilis, Otten & Rugg, 2001; Yovel & Paller, 2004). In comparison to the left parietal effect the mid-frontal effect appears to be insensitive to depth of encoding which is in line with behavioural findings, demonstrating no effect of depth of processing on know responses (e.g. Curran; 2000; Gardiner, Java & Richardson-Klavehn, 1996).

Study-test congruency of the presentation mode has been investigated in ERP studies in order to provide more insights in whether recollection and familiarity underlie distinct neural correlates. While ERP studies provide variable support the left-parietal effect varies with study-test congruency of mode of presentation ERP studies reported consistently a greater mid-frontal effect for a perceptual match relative to a mismatch regardless of the type of format (Ally & Budson, 2007; Curran, 2000; Curran & Clearly, 2003; Ecker et al., 2007; Groh-Bordin et al., 2006; Nyhus & Curran, 2009; Schloerscheidt & Rugg, 2004). The selective variation of the midfrontal effect as a function of perceptual match has been taken as further evidence that recollection and familiarity rely on distinct processes.

Moreover, fMRI studies have consistently provided evidence for functional dissociations between recollection and familiarity, particularly within the MTL (for review see Skinner & Fernandes, 2007; Yonelinas et al., 2005). There is extensive evidence that the hippocampus and perirhinal and parahippocampal regions play a different role in recollection and familiarity (for an alternative view see Wais, Wixted, Hopkins & Squire, 2006). While recollection has been associated with greater hippocampal activity, familiarity has been related to greater activity within the perirhinal cortex (e.g. Diana et al., 2007; Eichenbaum et al., 2007). Furthermore, the prefrontal cortex (PFC) is thought to play a different role for both kinds of processes (Duarte, Ranganath & Knight, 2005). Recent imaging analyses provide evidence that bilateral anterior frontal and bilateral superior frontal regions are selectively associated with recollection (Skinner, Grady & Fernandes, 2010). Moreover anterior PFC activity has been associated with the recollection of source information in previous imaging studies (e.g. Dobbins & Wagner, 2005; Kahn, Davachi & Wagner, 2004; Rugg et al.,

1998) and lesion studies (Janowsky, Shimamura & Squire, 1989; Wheeler, Stuss & Tulving, 1995). Those findings have led to the assumption that PFC activity may be associated with the recollection of contextual details (Skinner & Fernandes, 2007). In addition to familiarity-and recollection-related old-new effects, several late old/new effects starting around 800 ms after stimulus onset have been associated with post-retrieval processes such as evaluation processes and retrieval monitoring processes (for reviews see Rugg & Wilding, 2000; Cruse & Wilding, 2009; 2011).

1.6.2 NEURAL CORRELATES OF RECOLLECTION – THE REINSTATEMENT OF ENCODED PROCESSES

In line with the transfer appropriate processing framework neural models of episodic memory state that recollection depends on whether encoding-related patterns of brain activity are reinstated at retrieval (e.g. Alvarez & Squire, 1994; Norman & O'Reilly, 2003; Rolls, 2000). For instance, Norman and O'Reilly (2003) state that the CA3 region of the hippocampus encodes and stores the cortical activity associated with the processing and representation of a specific event. Recollection is associated with the reactivation of this stored representation pattern which leads to the reinstatement of the cortical activity patterns (for reviews see Danker & Anderson, 2010; Rugg et al., 2008). Importantly, a total overlap with the encoded activity is not necessary for the reactivation of the hippocampal representation, because a partial overlap can already lead to the reactivation of the entire representation. In accordance with those neural models, fMRI studies show growing evidence that the neural correlates of recollection are content-dependent and vary as a function of the nature of the encoding strategy (Johnson et al., 2009; Johnson & Rugg, 2007; Kahn et al., 2004; Nyberg, Habib, McIntosh & Tulving, 2000; Skinner et al., 2010; Vaidy, Zhao, Desmond & Gabieli, 2002; Wheeler, Buckner & Peterson, 2000; Wheeler, Shulman, Buckner, Miezin, Velanova & Peterson, 2006). The representation of two events may be associated with different types of content such as different sensory information that in turn leads to recollection processes that underlie different brain regions (Johnson & Rugg, 2007). For instance, neuroimaging studies (PET and fMRI) demonstrated that the sensory cortex was reactivated during retrieval depending on the encoded type of sensory information (e.g. Vaidya et al., 2002; Wheeler et al., 2003; Wheeler et al., 2006).

Moreover, there is evidence of reactivation of brain regions during the retrieval of emotional associations (e.g. Gottfried, Smith, Rugg & Dolan, 2004).

Recent neuroimaging studies that have investigated retrieval-related brain activity provide evidence that recollection of episodic information is associated with the reinstatement of encoded information. For instance, in Kahn et al. (2004) participants encoded visually presented words in either a visual imagery task or in an encoding task that emphasised phonological attributes. fMRI was only obtained at retrieval. At test, words that were encoded in the visual imagery task were associated with greater activity in the left parahippocampal cortical regions relative to words encountered in the phonological task. The reversed pattern was evident for activity in the left posterior frontal (premotor) cortex. In line with those findings, Woodruff, Johnson, Uncapher and Rugg (2005) demonstrated material-dependent patterns of brain activity in the left fusiform cortex as a function of whether words or pictures were recollected.

Crucially, the outlined neuroimaging studies only measured retrieval-related brain activity and only provide evidence that different brain regions were engaged during retrieval as a function of the type of encoding process. However, only studies that measure brain activity at both study and test within one experiment can provide strong support for the reactivation account (Johnson et al., 2009; Johnson & Rugg, 2007). Johnson and Rugg (2007) obtained fMRI signals at both encoding and retrieval. This study demonstrated that the reactivation of encoding-related regions is related to recollection by using the R/K procedure (Tulving, 1985). Participants encoded words either by generating sentences around the target words or imagined the object depicted by the word in the background scene. Both encoding-related and retrieval-related activity was obtained with fMRI. During retrieval, words that were encoded in the sentence task elicited greater activity in ventromedial prefrontal cortex. In contrast, words that were encoded in the imagery task were associated with greater activity in occipital and fusiform cortex. Crucially, these content-dependent regions overlapped partly with those regions that were initially activated when words were encoded in those two tasks. Interestingly, Johnson et al. (2009) demonstrated also reinstatement of encoding-related activity patterns for know judgements. Together, these findings are in line with the reinstatement models that state that recollection is influenced by the reinstatement of encoded processes (see also Johnson et al., 2009). Despite the fMRI evidence for the reinstatement of encoding-related processes, little

is known about the temporal characteristics of the reinstatement effects. Because of the low temporal resolution of the hemodynamic brain signals it is not clear whether the reinstatement of encoding-related processes is directly related to recollection processes or whether it is rather a consequence of the recollection. If the reactivation of encoding processes is directly associated with the recovery of episodic information, the reinstatement effect is expected to occur relatively early or at least accompanied by the recovery of episodic information (cf. Johnson, Minton & Rugg, 2008; Yick & Wilding, 2008).

Neuroscientific methods that have a high temporal resolution such as EEG are necessary to address these kinds of questions. Johnson et al. (2008) applied the same design as Johnson and Rugg (2007) to an ERP study. However, they obtained only retrieval-related activity. The authors demonstrated qualitatively different ERP old/new effects over frontal locations as a function of the encoded content. Words that were previously encountered in the sentence task elicited a larger frontally distributed old/new effect around 300 ms post stimulus than those that were studied in the imagery task. Thus, Johnson et al. (2008) showed initial evidence that content dependent brain activity may play a direct role in the recollection of episodic information. In this study content-dependent brain activity occurred in the same latency region as the left-parietal old/new effect that is thought to reflect generic recollection processes. In the same vein, Peters and Daum (2009) demonstrated that recollection-related ERP effects varied over frontal locations depending on the encoded content in a source memory paradigm. Despite this initial evidence it is unclear whether this activity reflects indeed the reinstatement of encoded-related activity, because encoding-related ERPs were not obtained and analysed. The acquisition of EEG data at encoding and retrieval could provide direct evidence for neural reinstatement. Moreover, neither of the reviewed studies manipulated directly the similarity of operations between encoding and retrieval to investigate whether the neural reinstatement is indeed stronger for study-test matches as proposed by the transfer-appropriate processing framework.

1.7 RESEARCH AIMS

My PhD research aimed to elucidate how the interaction between encoding and retrieval processes affects the neural correlates of human long-term memory. More specifically, the question was whether the degree of overlap between encoding and retrieval processes influences encoding- and retrieval-related brain activity. EEG was used throughout my PhD to dissociate between different fast acting cognitive processes and thus to understand both temporal and qualitative characteristics of the encoding-retrieval overlap.

Throughout my doctoral thesis the analyses of encoding-related brain activity and retrieval-related activity are focused on confident remember judgements which are thought to refer to the recollection of episodic memories. The restriction to confident remember responses aimed to avoid the posibility that differences as a function of encoding-retrieval overlap are confounded by differences in the type of recognition memory. In addition, brain activity related to remember responses is thought to refer to stronger memories and larger subsequent memory effects (e.g. Voss & Paller, 2009).

For the ease of understanding, the impact of encoding-retrieval overlap on encoding- and retrieval-related ERPs is presented in separate Chapters (Chapters 2 and 3). Crucially, the ERP approach does not enable to compare encoding-and retrieval-related ERPs in order to look at the impact of neural overlap which is expected to play an important role in recollection of episodic information (e.g. Norman & O'Reilly, 2003). Encoding-and retrieval-related ERPs are characterised by different types of neural signatures which makes it methodologically difficult to investigate the neural overlap between ERPs (Rugg et al., 2008; Norman, Polyn, Detre & Haxby, 2006). Therefore, Chapters 2 and 3 focus on how the overlap of cognitive operations between encoding and retrieval as proposed in the transfer-appropriate principle framework affect encoding and retrieval-related ERPs separately. The similarity of processes at encoding and retrieval was manipulated by varying the study-test congruency of presentation mode, the amount of perceptual information and the contribution of conceptual processes and perceptual processes at encoding and retrieval.

Three main questions were addressed. The first question was whether encoding-retrieval overlap of cognitive operations affects encoding-related brain activity (Chapter 2). Encoding-related ERPs were expected to vary as a function of the study-test congruency of presentation mode (word-word, picture-picture vs. word-picture, picture-word; Experiment 1). The transfer-appropriate processing account proposes that memory is influenced by the amount of perceptual and conceptual processes engaged at encoding and retrieval. Therefore, it was expected that the manipulation of the amount of perceptual processes at encoding and retrieval modulates the impact of study-test congruency on the encoding-related ERPs (Experiment 2). Further more, it was expected that the variation of conceptual and perceptual processes at retrieval influence the encoding-related ERPs (Experiment 3). Second, if encoding-retrieval overlap of cognitive operations plays a role in recollection, it was expected that retrieval-related ERPs differ with the amount of perceptual processes across encoding and retrieval (Chapter 3). Finally, analyses in the time and frequency domain provide the possibility to investigate the neural overlap of encoding and retrieval processes (e.g. Norman & O'Reilly, 2003). If reinstatement of encoding processes affects recollection of episodic information, oscillatory activity in the same frequency band across similar scalp locations was expected to be evident at encoding and retrieval as a function of study-test congruency (Chapter 4).

CHAPTER 2: DOES ENCODING-RELATED BRAIN ACTIVITY VARY WITH THE SIMILARITY OF COGNITIVE OPERATIONS BETWEEN ENCODING AND RETRIEVAL?

Experiment 1 has been published:
Bauch, E.M, & Otten, L.J (2011). Study–test congruency affects encoding-related brain activity for some but not all stimulus materials. *Journal of Cognitive Neuroscience*, in Press.

2.1.1 EXPERIMENT 1: THE INFLUENCE OF STUDY-TEST CONGRUENCY OF PICTURES AND WORDS ON THE NEURAL CORRELATES OF ENCODING

Whether we remember an event depends on the degree of overlap between encoding and retrieval operations. The transfer appropriate principle framework (Roediger, 1990) claims that the more encoding processes are recapitulated at retrieval, the more likely it is that an event will be remembered. For instance, Morris et al. (1977) demonstrated that memory performance following semantically-encoded words is best when the retrieval cue emphasized semantic processing. In contrast, memory performance was better for phonologically encoded words, when they were subsequently tested with a memory test that engaged phonological processes. Thus, it is not solely the level of processing at encoding (i.e. depth of encoding, Craik & Lockhart, 1972) that determines memory success, but also the interplay between encoding and retrieval. Behavioural studies that manipulated the physical similarity of the mode of presentation across study and test showed good support for the transfer appropriate processing principle. A perceptual match of the presentation mode across study and test led to higher memory performance than when memory was probed with incongruent cues (e.g. Mulligan & Osborn, 2009; Mintzner & Snodgrass, 1999; Weldon & Roediger, 1987).

Despite the strong evidence in behavioural findings, little is known about the role of study-test congruency in the neural base of long-term memory (Rugg et al., 2008). It is not clear how the congruency of functional processes between encoding and retrieval affects the neural correlates of encoding. This question will help understand the nature of encoding-related activity and will have relevant implications in terms of understanding differences in encoding-related activity between certain populations (i.e. different age and patient groups).

Little is known about how encoding-related brain activity is affected by study-test congruency. Previous work has shown that there is not a single activity pattern that reflects encoding success, but it rather varies depending on the type and material at encoding (Baker et al., 2001; Davachi et al., 2003; Fletcher et al., 2003; Mitchell, Macrae, & Banaji, 2004; Otten & Rugg, 2001a, b). This is in line with the transfer-appropriate principle suggesting that memory representations for the same event can differ depending on what kind of features the encoding process was focused on. Moreover, the transfer-appropriate processing theory premises that an event will be most likely remembered when the retrieval cue overlaps with those features that were initially used to create a memory representation of the event. Therefore, encoding-related brain activity may not only be determined by the processing types and attributes that are emphasised during encoding, but also by the type of retrieval cue. A few studies indeed show evidence that encoding-related activity varies depending on how memory is later probed (Bridger & Wilding, 2010; Otten 2007, Park & Rugg, 2008; Wimber et al., 2010). In an event-related fMRI study Otten (2007) showed evidence that different brain regions predicted successful memory encoding for visually presented words depending on whether memory was tested with an auditory word or a picture. In the same vein, Bridger and Wilding (2010) reported that electrical encoding-related brain activity was influenced by the type of retrieval requirements. In both, Otten (2007) and Bridger and Wilding (2010), it was proposed that the brain activity observed at encoding refers to the encoding processes of those stimulus attributes that are necessary for successful retrieval.

Although the reviewed studies show evidence that encoding-related brain activity varies as a function of the type of retrieval cue, it is unclear whether the type of retrieval process or the congruency between encoding and retrieval determines encoding-related activity. The present experiment aimed to address this question. A similar question was addressed with fMRI (Park & Rugg, 2008). In Park and Rugg (2008) words and pictures were encountered in an incidental encoding task. At test, half of the studied items were presented in the same mode of presentation as during study (i.e. picture-picture; word-word) and half of the items were shown in the alternative mode of presentation (i.e. picture-word; word-picture). Park and Rugg (2008) pinpointed material-specific brain regions where the brain activity was greater for subsequently recognised items that were later probed in the congruent format in comparison to when study and test format mismatched. Thus, this finding showed initial evidence that study-test congruency plays some role in the neural correlates of memory encoding.

However, the temporal characteristics of hemodynamic brain signals restrict the conclusions that can be drawn. Due to the slow temporal resolution of fMRI it is not clear whether the study-test congruency plays a direct role in memory encoding or whether it is rather a consequence of the encoding process. If study-test congruency affects indeed the memory formation process, the modulations would be expected fairly early after item onset (Cameron, Yashar, Wilson, & Fried, 2001). In the present experiment EEG was used that has a high temporal resolution to investigate how study-test congruency affects the timing and nature of encoding-related brain activity. The present experiment manipulated the physical similarity of the presentation mode between study and test in order to investigate the influence of encoding and retrieval overlap on the electrical brain activity at encoding. Park and Rugg (2008) and previous behavioural studies (e.g.Mulligan & Osborn, 2009; Mintzner & Snodgrass, 1999) showed consistently that memory benefits from a format overlap between study and test.

In Experiment 1, a series of words and pictures were incidentally encoded in a size judgement task. After a delay memory was tested with a recognition test. Half of the participants saw all studied items in the same presentation mode as during encoding (i.e. words-words, pictures-pictures) and the other half were presented with all studied items in the alternative presentation mode (i.e. words-picture, pictures-words). The study-test overlap was manipulated between groups in order to have an acceptable signal-to-noise ratio to look at the subsequent memory effect of each combination (i.e. picture-picture; word-word; picture-word; word-picture). Pilot work indicated that not enough pictures would be forgotten when probed with pictures in a within-subjects design. Moreover, in Park and Rugg (2008), the picture-picture condition was on average associated with only seven forgotten items (see their Table 2). Therefore, study-test congruency was manipulated between-subjects to increase the number of trials in each condition.

The recognition test differentiated between R/K responses (Tulving, 1985) to dissociate different types of recognition memory (dual process theory: recollection versus familiarity Yonelinas, 2002; for caveats see e.g. Wais et al., 2008). Due to the experimental design a rich data set was created that has the power to investigate how the brain activity related to the different memory types varies according to the degree of encoding-retrieval overlap. Here, brain activity only related to remember responses was considered to avoid the possibility that study-test congruency effects would be confounded by different types of recognition judgments. Brain activity related to remember responses is thought to reflect recognition memory based on recollection or strong memories (Yonelinas, 2002). Previous studies demonstrated that remember responses are associated with stronger subsequent-memory effects (e.g. Friedman & Trott, 2000; Mangels, Picton & Craik, 2001; Voss & Paller, 2009). Only a subset of the participants had enough know trials (i.e. > 14 trials). Therefore, throughout the PhD thesis only brain activity related to remember responses was analysed.

Brain activity related to encoding success was measured with the subsequent memory approach (Sanquist et al., 1980) which is a well established approach to dissociate encoding related processes from activity related to other cognitive processes. The question of interest was whether the subsequent memory effect would differ as a function of whether the presentation mode at study and test were congruent or incongruent. On the one hand, the same brain activity might be engaged and only vary in its degree as a function of study-test congruency. This finding would suggest

that similar processes may be engaged irrespective of the study-test congruency. On the other hand, qualitatively different processes might be engaged. According to the transfer appropriate processing, encoding-activity reflects most likely these types of encoding processes that overlap with the retrieval cue. For instance, while a word cue at test may be beneficial if encoding emphasised semantic processes, picture cues may overlap best with items that were processed more perceptually at encoding. These distinct encoding processes would be associated with qualitatively different subsequent memory effects. Although the neural source of the electrical brain activity is very difficult to determine (Nuñez, 1981), topographical differences would indicate qualitatively different encoding-related processes are engaged as a function of study-test congruency (Otten & Rugg, 2004). Moreover, if study-test congruency plays a direct role in memory encoding it was expected that study-test congruency effects would be evident immediately or briefly after item onset.

2.1.2 METHODS

PARTICIPANTS

The experimental procedures were approved by the University College London Research Ethics Committee. Subjects were right-handed and native English speakers as assessed by self report. The analyses are based on the data of 48 subjects. Half were randomly assigned to the match group (mean age: 23 years; age range: 19-34 years; 15 women) and half to the mismatch group (mean age: 23; age range: 18-34; 15 women). The data from a further 11 volunteers were excluded due to electrooculogram (EOG) artefacts (n = 3) and insufficient numbers of trials because of extreme high or low memory performance (n = 8, criterion was at least 14 trials in each condition).

All participants gave written informed consent and were paid £ 7.50/hour for participation. All of them reported normal or corrected-to-normal vision and no neurological or psychiatric histories.

STIMULUS MATERIAL

Stimuli were drawn from a pool of 411 black-and-white pictures of everyday objects (e.g. tools; white goods) and animals, and their corresponding names. All of the words were between three and eleven letters in length. Three sets of 128 pictures and 128 words were selected pseudo-randomly, keeping the word lengths across the word sets approximately equal. The sets were counterbalanced across participants in such a manner that each item was presented equally often as a picture or word during the study phase and as an unstudied word or unstudied picture during the test phase.

One half of the objects represented by the pictures and words in each set could fit in a shoebox – in real size-, and the other half of items were bigger than a shoebox. The stimuli were assigned to the 'Fit' or 'Not Fit' condition based on the subjective judgement of the experimenter. Because of the subjective nature of the task, task accuracy was not considered in the behavioural analyses.

A study list contained 128 words and 128 pictures that were randomly intermixed (256 critical items) and 4 additional filler items (2 words and 2 pictures) at the beginning of each block. Filler items were not included in the behavioural and ERP analyses. Test lists consisted of all studied items (128 words and 128 pictures) and 128 new items (64 words and 64 pictures), along with 6 fillers (3 words and 3 pictures). In total, 384 critical items were presented at test. Participants of the match group were shown all of the studied items in the same format at test as during study (i.e. picture-picture; word-word). All of the studied items at test were presented in the alternate format at test as during study in the mismatch group (i.e. picture-word; word-picture).

Blocks of 64 items each were created for both study and test lists. The remaining items in the stimulus pool were used for practice lists. All items were presented in central vision on a white background for 1 s. Words were shown in a black Helvetica font.

PROCEDURE

The experiment consisted of an incidental study phase and a surprise recognition memory test after a one hour delay (see Figure 2). After the electrode application the subjects sat in front of a computer monitor.

At study, a series of words and pictures were randomly intermixed and occurred equally often. Preceding cues informed the participant about the format of the upcoming item ('W' for a word; 'P' for a picture). The cues were written in red and started 1.5 sec before stimulus onset (1.4 sec presentation duration, 100 ms blank periods between preparatory cue and item). Trials were separated by fixation crosses (+). The time between the items' offset and the cues onset varied randomly between 1.5 and 3 sec. During the study phase, the volunteers were not aware that their memory would later be tested. Volunteers were asked to focus on the cue (i.e. 'P' or 'W') to prepare for the upcoming item. By pressing one of two buttons they decided whether or not the presented object would fit in a shoebox – in its real size. They were instructed to respond as quickly and as accurately as possible with their left or right index fingers depending on their decision. The responding hand was counterbalanced across the participants. A short practice list was given prior to the study phase. The study phase was split in four blocks of 64 trials each. The blocks were separated by short rest periods. The study phase took approximately 25 minutes.

The test phase followed the study phase after approximately one hour. At this point, volunteers found out that their memory would be tested. All studied items were presented again, intermixed with unstudied items (half words and half pictures). Again, red cues starting 1.5 sec before each test item indicated in which format the following item would appear ('W' for a word; 'P' for a picture). Volunteers were instructed to attend the cues in order to prepare for the format of the upcoming item. A fixation cross filled the interval between the test item and the following cue. The time between the item offset and cue onset varied randomly between 2.5 and 4 sec.

Volunteers were asked to make an R/K judgement about each test item by pressing one of three buttons (Yonelinas & Jacoby, 1995). If subjects were confident that they have seen the item before and could recollect one or more specific details about the item presentation during the study phase, they were instructed to respond with the finger corresponding to the 'remember' response. If they only knew confidently that the item had been presented during study without recollecting specific

details, they were asked to press the 'know' button. If the test item was new, they had to give a 'new' response. To minimise contamination by lucky guesses, participants pressed also 'new' in cases when volunteers were not confident about whether they had seen the test item previously or not. The mapping of the responding fingers (i.e. index finger, middle finger and ring finger of the right hand) and corresponding decisions (i.e. remember, know, new) was randomised across subjects. Volunteers in both groups were instructed to give memory judgments irrespective of whether the studied item appeared in the same format as during the study phase or in the alternate format (e.g. whether a picture of a 'bee' was now presented as the word 'bee' or as a picture of a 'bee'). Again, both accuracy and speed were stressed. A practice block preceded the test phase to familiarise participants with the recognition task. The test phase was divided in six blocks of 64 trials each and was around an hour in length.

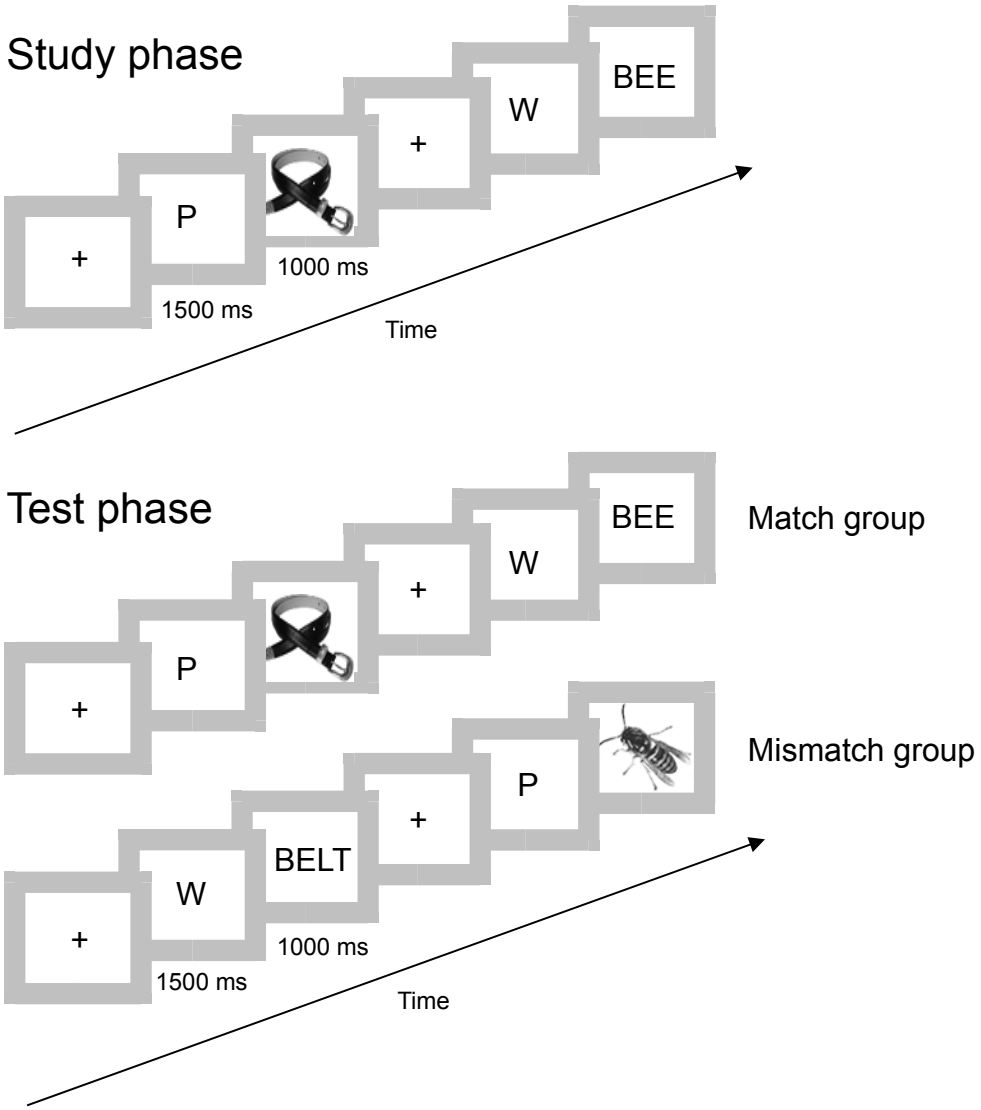

Figure 2. EXPERIMENTAL PROCEDURE OF STUDY AND TEST PHASE. Photographs and words were presented at study and test. Cues indicated the upcoming item type. The study phase consisted of an incidental encoding task (size judgement). At test, half of the participants (match group) saw all studied items in the same mode of presentation (picture-picture; word-word) and half of the participants saw all studied items in the alternative mode of presentation (picture-word; word-picture). The memory test incorporated R/K judgements.

EEG ACQUISITION

The Electroencephalogram (EEG) was recorded from 32 scalp sites using silver/silver-chloride electrodes fitted in an elastic cap according to an equidistant electrode montage (see Figure 3 for montage 10 at www.easycap.de /easycap/e/electrodes /13 _ M10.htm) and from two additional electrodes placed on the right and left mastoids. Vertical eye movements (VEOG) were recorded bipolarly above and below the right eye. Electrodes at the outer canthi picked up the horizontal eye movements (HEOG). All data were recorded relative to a midfrontal site. The impedance level was kept below 5 kΩ. All signals were amplified with a set of Contact Precision amplifiers, band-pass filtered between 0.01 and 35 Hz (3dB roll-off), and digitized (12-bit resolution) at a rate of 500 Hz.

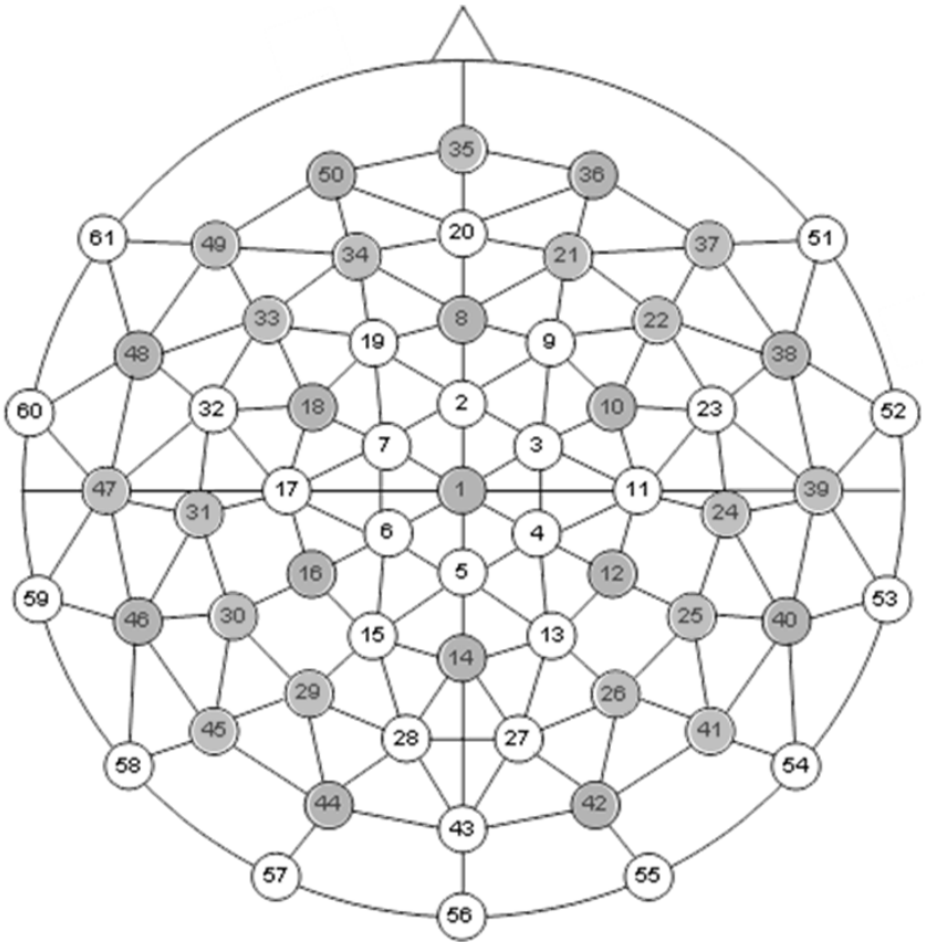

Figure 3. EQUIDISTANT ELECTRODE MONTAGE. Montage 10 at www.easycap.de/easycap/e/electrodes/13_M10.htm.The 32 scalp electrodes that were used are highlighted in grey.

BEHAVIOURAL DATA ANALYSIS

To dissociate the different types of recognition memory, the calculation of the memory performance was based on the assumption that recollection and familiarity are distinct processes (Yonelinas & Jacoby, 1995; Park & Rugg, 2008). The probability of recollection was calculated by subtracting the proportion of false alarms (i.e. incorrect remember judgements for new items) from the proportion of hits (i.e. correct remember judgement for old items) [Pr Hit-Pr FA]. The probability of familiarity was estimated by subtracting the division of the proportion of know hits with 1 minus the proportion of remember hits from the decision of the proportion of false alarms for know responses with 1 minus the proportion of false alarms of remember judgements[(Pk Hit/(1-Pr HIT))-(Pk FA/(1-Pr FA))].

EEG DATA ANALYSIS

Signals were digitally filtered offline between 0.05 and 20 Hz (96 dB roll-off), down sampled to 125 Hz, and algebraically re-referenced to averaged mastoids (re-instating the online reference site). The length of the EEG epoch for the study and test data extended from 100ms before an item to 1948 ms after item onset.
The ERP waveforms were created for each subject and each electrode site separately for pictures and words in the match and mismatch groups. Epochs including drifts exceeding ±50 μV, horizontal eye movements, muscle artifacts and amplifier saturations were excluded from the averaging process. Averaged ERPs in each condition were based on a minimum of 14 artifact-free trials to assure a satisfactory signal-to-noise ratio. The mean number of remember trials for pictures and words in the match group were 45 (range 16-74) and 49 (18-83). The mean number of forgotten trials for the corresponding conditions were 34 (14-76) and 29 (15-54). The mean number of remember trials for pictures and words were 44 (22-96) and 49 (14-84) and 40 (14-69) and 39 (14-80) for forgotten trials for the mismatch group. Only a subset of participants had at least 14 artifact-free trials for items given know judgments (17 in the mismatch group and 20 in the match group). This response category was therefore not considered in isolation. An additional analysis was performed where remember and know responses were collapsed. This analysis showed the same pattern of results as I report in this Chapter, except that the effects were smaller and statistically weaker. To investigate how ERPs during encoding vary according to the degree of study-test

congruency, the subsequent memory effect (i.e. subsequently remembered vs. later new judgements) as index of successful memory formation was compared between the match and mismatch groups for both stimulus formats. Statistical reliability of differences in time, amplitude and scalp distribution across conditions was tested with repeated measures analyses of variance (ANOVAs). Statistical comparisons of the mean amplitude in μV were conducted with the between-subjects factor of group (match/mismatch) and the within-subjects factors of item type (word/picture), subsequent memory (remembered/forgotten), and electrode site (all 32 electrodes, see Figure 3). Only analyses involving a significant subsequent memory effect are reported. In case of significant interactions follow-up analyses were conducted to understand the nature of the effect.

Where necessary (i.e. factors with more than 2 levels) the reported p-values and degrees of freedom (dfs) represent Greenhouse-Geissler corrected values to control for non-sphericity (Keselman & Rogan, 1980). Additionally, to establish the significance of scalp topography differences according to the degree of overlap, the scalp distributions were statistically compared after scaling the data with the max/min method over 32 electrodes (see figure 2) to reduce confounding influence of overall amplitude differences (McCarthy & Wood, 1989). The max/min method was used to equate amplitudes between groups and conditions, because alternative scaling methods such as the vector method have been associated with interpretational problems (Haig, Gordon, & Hook, 1997; Urbach & Kutas, 2006, 2002; Wilding, 2006). The max/min method was applied to the difference wave (remember minus forgotten) of the 46 participants for each of the four experimental conditions (picture-picture; word-word; word-picture; picture-word) and included all 32 electrode sites. Repeated measures ANOVAs were conducted to test whether similar pattern of results were found as on the unscaled data.

2.1.3 RESULTS

BEHAVIOURAL DATA

ENCODING TASK

Because the encoding task was based on subjective judgments, only RT data were analysed. The mean RTs for pictures were 841 ms (standard deviation [SD] = 136 ms) and 811 ms (SD = 151 ms) for the match and mismatch groups respectively. The shoebox task for words was performed with an RT of 830 ms (SD = 106 ms) and 814 ms (SD = 151 ms) in the match and mismatch groups. An ANOVA comparing mean RTs across groups and item types did not reveal significant differences, *p*s > .316. RT across groups and item types did also not differ depending on whether the item was subsequently remembered or forgotten; *p*s > .072.

MEMORY TEST

The proportions of hits and false alarms corresponding to remember and know responses and the estimations of recollection and familiarity separated according to the format in the match and mismatch groups are shown in Table 1 and Table 2. The ANOVA on the accuracy data with the between-subject factor group (match vs. mismatch) and the within-subject factors memory type (recollection vs. familiarity) and format (word vs. picture) resulted in a significant main effect of group ($F(1, 46) = 13.84$; $p = .001$), suggesting higher overall memory performance for the match group (mean [M] = .38) irrespective of the type of stimulus format (M = .30).

Remember responses for congruent cues were given more quickly than for incongruent cues, although this difference just failed to be significant ($F(1, 46) = 4.03$, $p = .051$; see Table 3). Overall, the behavioural findings provide good support for transfer-appropriate processing, because the overall memory performance was better for items that were later cued with the congruent mode of presentation than items that were probed with the incongruent mode of presentation.

Table 1. Recollection and familiarity estimates for photographs and words that were cued in the congruent (match group, N=24) and incongruent (mismatch group, N=24) mode of presentation.

Study type	Test type	Recollection	Familiarity
Picture	Picture	0.36 (0.11)	0.38 (0.18)
	Word	0.31 (0.12)	0.23 (0.11)
Word	Word	0.39 (0.12)	0.39 (0.15)
	Picture	0.35 (0.14)	0.29 (0.17)

Values are across-subject means (SD).

Table 2. Recognition performance for words and pictures cued in the same mode of presentation at test (match group) and in the alternative mode of presentation (mismatch group).

Group	Item type	Remember	Know	New
Match	Old word	0.43 (0.14)	0.32 (0.15)	0.25 (0.08)
	Old picture	0.40 (0.14)	0.31 (0.16)	0.29 (0.11)
	New word	0.03 (0.03)	0.13 (0.10)	0.84 (0.11)
	New Picture	0.04 (0.03)	0.09 (0.06)	0.87 (0.07)
Mismatch	Old word	0.44 (0.16)	0.22 (0.13)	0.34 (0.14)
	Old picture	0.39 (0.15)	0.25 (0.12)	0.36 (0.14)
	New word	0.08 (0.08)	0.15 (0.11)	0.77 (0.16)
	New Picture	0.09 (0.07)	0.18 (0.12)	0.73 (0.14)

Values are across-subject means (SD).

Table 3. Mean RT (ms) for words and pictures cued in the same mode of presentation at test (match group) and in the alternative mode of presentation (mismatch group).

Group	Item type	Remember	Know	New
Match	Old word	976 (195)	1161 (312)	1098 (293)
	Old picture	997 (239)	1141 (314)	1078 (278)
	New word	840 (544)	1157 (420)	1032 (245)
	New Picture	790 (528)	1115 (519)	1020 (262)
Mismatch	Old word	1130 (243)	1347 (346)	1367 (384)
	Old picture	1094 (204)	1315 (337)	1258 (334)
	New word	954 (518)	1315 (444)	1190 (282)
	New Picture	1044 (436)	1313 (446)	1304 (336)

Values are across-subject means (SD).

EVENT-RELATED POTENTIALS

Encoding-related ERPs elicited by later remembered and forgotten items were compared between groups to establish study-test congruency effects on the neural correlates of successful encoding. Group averaged ERPs elicited by later remembered and forgotten responses for studied words and pictures, in the match and mismatch group are shown in Figure 4.

For words, ERPs associated with remember responses were more positive-going than forgotten items at frontal scalp electrodes. The positive-going modulation emerged around 700 ms and persisted until around 1300 ms. For pictures that were subsequently tested in the congruent presentation mode the subsequent memory effect was also most pronounced over frontal sites and emerged 100 ms after item onset. In contrast, studied pictures that were later tested with a word were associated with a positive-going modulation over parietal sites. The positive-going modulation for pictures in the incongruent condition emerged also early, around 100ms after picture onset, and was sustained until the end of the epoch.

Statistical analyses confirmed these observations. Repeated measures ANOVAs on mean amplitudes were conducted separately for 100-700 ms, 700-1300 ms, and 1300-1900 ms intervals. The latencies are based on visual inspection of the subsequent memory effect in the group averaged ERPs to statistically test whether this effect is consistent across subjects (see Figure 4). The use of three latency regions allow the statistical analysis of the small modulation for studied words in the middle time region, but also enable to test for the early and sustained modulations for studied pictures. In the ERP literature, the subsequent memory effect is sustained over time and its onset and offset is not well defined (for review see Johnson & Friedman, 2000). Despite the sustained modulation for pictures from 100 ms to 1900 ms the division in three smaller time regions allowed to test for possible differences over time. However, the analyses across time regions did not reveal any significant differences. Thus, only the separate analyses for each of the three latency regions are reported. Table 4 and Table 5 display the statistics of the comparisons of mean amplitudes between groups and conditions.

The ANOVA gave rise to significant four-way interactions between group, item type, subsequent memory and electrode site in all three latency regions (Table 4). The interaction in the first interval remained significant after scaling the data, $F(3.7, 170.3) = 2.69$, $p = .037$. Subsidiary analyses separately on each item type were conducted to understand the interaction. For studied words, the analyses revealed no significant subsequent memory differences between groups in any of the three time intervals (ps > .476). However, a main effect of subsequent memory and an interaction with site that approached significance ($p = .064$) was evident in the middle time interval, between 700-1300 ms. In the previous literature subsequent memory effects associated with deep encoding processes are usually reported over frontal electrode sites (Friedman & Johnson, 2000; Otten, Sveen & Quayle, 2007). Therefore, a direct analysis of five anterior electrode sites (21, 34, 35, 36, and 50; see Figure 3 for montage) confirmed a frontal positive-going modulation for words irrespective of study-test congruency $F(1, 46) = 7.68$, $p = .008$ (for spline map see Figure 6).

In comparison to words, pictures gave rise to significant interactions between group, subsequent memory and electrode site in all three time intervals (Table 5). These interactions were still found for the 100-700, 700-1300, and 1300-1900 ms intervals after scaling the data ($F(3.9, 180.4) = 6.61$, $F(5.0, 231.2) = 8.34$, and $F(4.5, 206.2) = 6.86$; all $p < .0001$). Further analyses on the picture data in the match and mismatch groups gave rise to significant interactions between subsequent memory and site in all three intervals. Those effects were also observed after scaling the data. The statistics for the match group were $F(3.1, 70.9) = 8.02$, $F(3.2, 74.6) = 10.34$, and $F(3.4, 77.9) = 6.60$, all $p < .0001$ and for the mismatch group $F(4.2, 110.0) = 3.62$, $F(4.3, 97.9) = 4.73$, and $F(4.5, 104.6) = 3.36$, all $p < .009$. Figure 4 shows the scalp distribution of the subsequent memory effects elicited by pictures in both groups. The subsequent memory effects for the match group were only significant over frontal sites and not posterior locations. In contrast, for the mismatch group, effects over posterior sites revealed only significant positive-going modulations and not over frontal locations (see Table 4 and 5 for statistics and Figure 5 for scalp distribution map).

Table 4. F statistics and *p* values of key effects in the across-group ANOVAs on electrical brain activity.

		Latency Interval		
Item type	Effect	100-700	700-1300	1300-1900
	IT x GP x SM x ST	$F(3.6, 166.0) = 6.15$, $p < .0001$*	$F(4.3, 196.6) = 4.73$, $p = .001$	$F(4.1, 187.8) = 3.21$, $p = .014$
Words	GP x SM x ST	$F(3.8, 174.7) = 0.82$, $p = .508$	$F(3.6, 166.8) = 0.67$, $p = .600$	$F(4.3, 198.5) = 0.89$, $p = .476$
Pictures	GP x SM x ST	$F(3.7, 169.3) = 7.65$, $p < .0001$*	$F(4.1, 189.0) = 11.82$, $p < .0001$*	$F(4.2, 194.4) = 7.42$, $p < .0001$*

Degrees of freedom and *p* values are Greenhouse-Geisser corrected. GP = group; IT = item; SM = subsequent memory; ST = electrode site. * = significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985).

Table 5. F statistics and *p* values of the key effects in the within-group ANOVAs on picture-related activity.

		Latency Interval		
Group	Effect	100-700	700-1300	1300-1900
Match	SM x ST	$F(3.1, 70.9) = 8.02$, $p < .0001$*	$F(3.2, 74.3) = 10.29$, $p < .0001$*	$F(3.4, 77.9) = 6.60$, $p < .0001$*
	SM anterior sites	$F(1, 23) = 15.37$, $p = .001$	$F(1, 23) = 26.06$, $p < .0001$	$F(1, 23) = 11.47$, $p = .003$
	SM posterior sites	$F(1, 23) = 0.21$, $p = .654$	$F(1, 23) = 2.70$, $p = .115$	$F(1, 23) = 0.05$, $p = .821$
Mismatch	SM x ST	$F(4.1, 93.7) = 3.34$, $p = .013$*	$F(4.5, 102.6) = 6.85$, $p < .0001$*	$F(4.5, 104.6) = 3.36$, $p = .009$*
	SM anterior sites	$F(1, 23) = 1.30$, $p = .267$	$F(1, 23) = 3.60$, $p = .071$	$F(1, 23) = 4.20$, $p = .052$
	SM posterior sites	$F(1, 23) = 12.45$, $p = .002$	$F(1, 23) = 31.14$, $p < .0001$	$F(1, 23) = 20.85$, $p < .0001$

Degrees of freedom and *p* values are Greenhouse-Geisser corrected. SM = subsequent memory; ST = electrode site. * = significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985). Anterior sites refer to the five most frontal electrodes in the montage (sites 21, 34, 35, 36, and 50 of montage 10 at http://www.easycap.de/easycap/e/electrodes/13_M10.htm). Posterior sites refer to five equivalent parietal ones (sites 12, 14, 16, 26, 29).

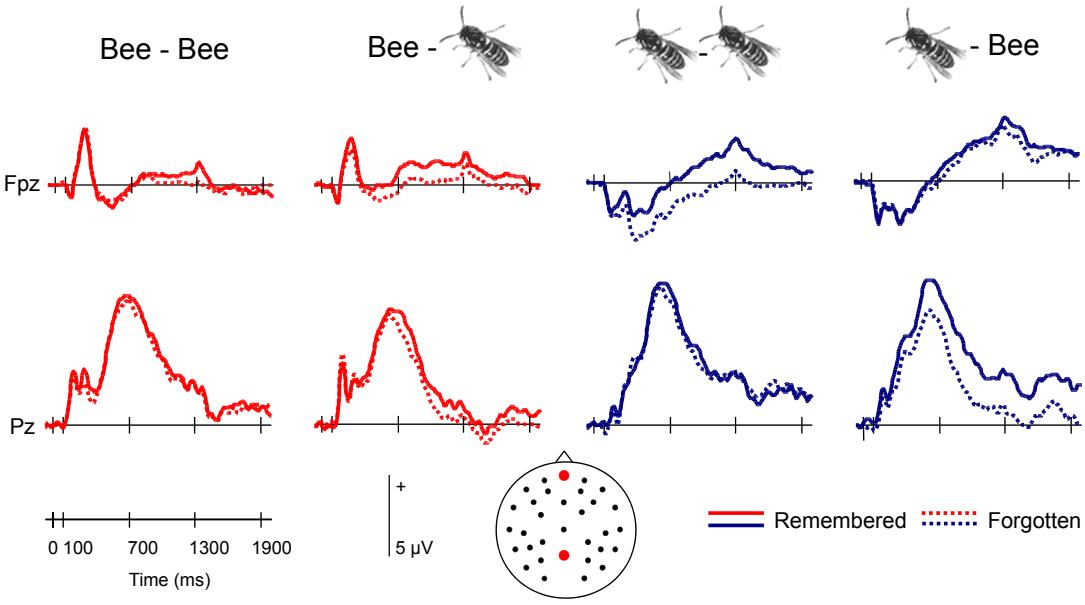

Figure 4. Encoding-related neural activity. Group averaged ERP waveforms elicited by encoded words and pictures later probed in the same mode of presentation (match group) and different mode of presentation (mismatch group). Waveforms are compared for later remembered (solid line) versus forgotten (dotted line) words (highlighted in red) and pictures (highlighted in blue) in the match and mismatch group and displayed for two representative midline electrode sites (equivalent to Fpz and Pz of the international 10/10 system). Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes.

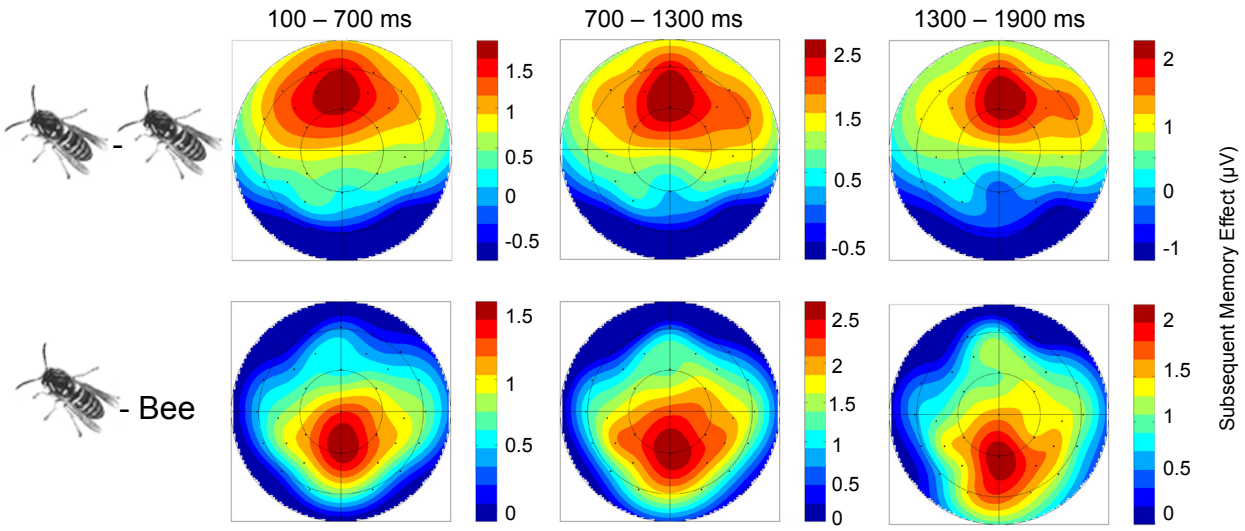

Figure 5. The spline maps illustrate the scalp distribution of the difference activity between subsequently remembered and forgotten pictures in the match (top) and mismatch group (bottom) in the latency region of 100-700 ms, 700-1300 ms and 1300-1900 ms.

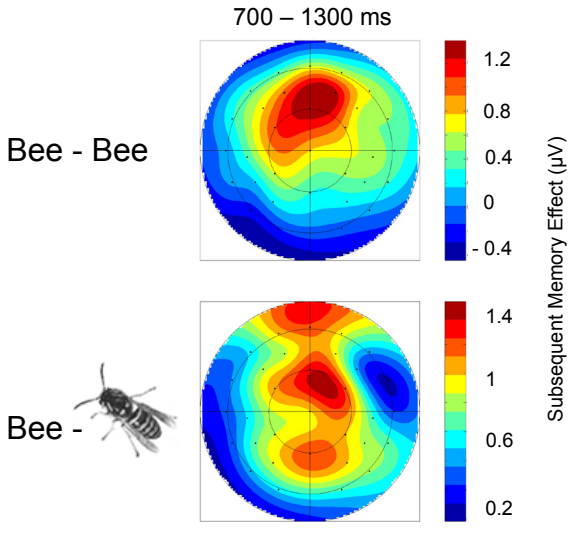

Figure 6. Scalp distributions of the ERP difference between later remembered and forgotten words in the match (top) and mismatch group (bottom).

2.1.4 DISCUSSION

Experiment 1 manipulated the degree of similarity between study and test formats to investigate how neural correlates of encoding vary depending on the degree of study-test overlap. The overall memory performance was as expected better for the match than mismatch groups for both words and pictures. Thus, the behavioural findings provide good support for the transfer-appropriate processing principle (Roediger, 1990; Tulving & Thomson, 1973). In line with previous studies, the findings demonstrate that memory retrieval benefits from an overlap between encoding and retrieval processes (Jacoby, 1996; Mulligan & Osborn, 2009; Leboe et al., 2005; Park & Rugg, 2008; Schloerscheidt & Rugg, 2004; Stenberg et al.,1995).

The ERP data provide strong support that study-test congruency also has an effect on the neural correlates of encoding. In accordance with the transfer-appropriate processing principle (Roediger, 1990; Tulving & Thomson, 1973) encoding-related ERP activity differed qualitatively depending on whether the retrieval cue was incongruent or congruent to the studied mode of presentation. However, study-test congruency had an effect on the neural correlates of memory formation as a function of item type. While for words a positive-going modulation over frontal locations was found irrespective of study-test congruency, for pictures subsequent memory effects differed in terms of scalp distribution from around 100 ms as a function of type of retrieval cue. Pictures that were later cued with pictures elicited a frontally distributed subsequent memory effect. In contrast, encoded pictures that were subsequently probed with a word showed a posteriorly distributed subsequent memory effect.

Three main conclusions can be drawn from these findings. First, the interplay between encoding and retrieval processes affects the neural correlates of encoding. To my knowledge, this is the first study showing that electrophysiological correlates of encoding vary as a function of encoding-retrieval overlap. Thus, encoding-related brain activity is not only defined by the type of encoding or retrieval process, but also the overlap between both processes. Second, study-test congruency plays a direct role in long-term memory, because subsequent memory effects varied as a function of study-test congruency shortly after item onset. Third, the material-specificity of this effect suggests that encoding-retrieval overlap is not a universal organisational principle of the neural correlates of encoding. This will be discussed in more detail throughout the discussion.

The findings are in line with previous studies suggesting that encoding-related activity differs depending on how memory is subsequently probed (Bridger & Wilding, 2010; Davachi et al., 2003; Otten, 2007; Ranganath et al., 2004). As outlined in the introduction, modulations of encoding-related activity as a function of the type of retrieval cue may arise because of distinct attributes of the encoded episode. Thus, encoding-related activity most likely represents the processing of those attributes that are necessary for the successful retrieval of an event. Memory benefits when attributes at encoding are again emphasised at retrieval (Craik & Lockhart, 1972). Thus, encoding-related activity reflects the processing of those attributes that overlap with those at retrieval (Otten, 2007; Rugg et al., 2008).

In contrast to a previous fMRI study (Park & Rugg, 2008) the high temporal resolution of EEG in Experiment 1 allows the detection of the temporal occurrence of the study-test congruency effect. Encoding-related activity varied as a function of study-test congruency directly after stimulus onset (~100 ms) and persisted until the end of epoch. The early occurrence of this study-test modulation, suggests a direct role of encoding-retrieval overlap for the neural correlates of memory formation (Cameron et al., 2001).

Interestingly, the ERP findings are only partly in line with the fMRI data of Park and Rugg (2008). They reported that brain activity was influenced by study-test congruency for both words and pictures. The different findings may be related to methodological differences. Electromagnetic and hemodynamic brain signals reflect different kinds of activities and it is not clear whether the ERPs in Experiment 1 and fMRI signals tap into the same type of processes (Otten & Rugg, 2004). The low temporal resolution of fMRI signals does not allow any conclusions about whether the study-test congruency effects in Park and Rugg (2008) refer to encoding-related processes or to processes downstream of encoding. Moreover, the design of both studies differed in various ways. For instance, while Park and Rugg (2008) only compared activity related to correctly recognised items across match and mismatch conditions, the present design measured differences in subsequent memory effects (i.e. remembered vs. forgotten items). Furthermore, Park and Rugg (2008) used an outdoor/indoor incidental encoding task and manipulated study-test congruency within subjects, while the present experiment used a size judgment incidental encoding task and a study-test congruency manipulation across subjects. Together, the

type of acquisition technique and differences in experimental parameters may explain the different patterns of results in Experiment 1 and Park and Rugg (2008).

What is the functional role of the qualitatively different subsequent memory effects as a function of study-test congruency? No general signature of study-test congruency was found, because the effect of encoding-retrieval overlap on encoding-related activity was material-specific. Thus, the mere match or mismatch of presentation modes does not determine the type of attributes that are crucial for encoding-related brain activity. Studied words elicited a positive-going modulation over anterior locations irrespective of the degree of study-test congruency. In a number of ERP studies, a frontal subsequent memory effect was consistently established for words. This effect is usually associated with semantic or associative processes that are engaged at encoding (see for review Johnson & Friedman, 2000; Otten et al., 2007; Weyerts et al., 1997). Therefore, words that were encoded with an emphasis on semantic attributes were most likely to be remembered in the recognition test. It is not surprising that retrieval of encoded words later cued with words relied on semantic processes. But why would retrieval in the word-picture condition rely on the processing of semantic attributes? At encoding, participants probably engaged mental imagery strategies during the size judgement task. Previous studies provide evidence that size judgement tasks indeed engage mental imagery (Kosslyn, 1975). Although pictures at retrieval might emphasise perceptual attributes, the perceptual overlap between the mental image at study and the actual picture at test in the word-picture condition may have been small. The internal image most likely differed from the picture actually presented at test (Nelson, Reed, & McEvoy, 1977). Therefore, the best retrieval strategy in the word-picture condition would have been to rely on the overlap in conceptual attributes between encoding and retrieval.

For pictures, qualitatively different subsequent memory effects were found depending on the congruency between study and test presentation modes. When pictures were probed with a picture at test, a positive-going modulation over anterior sites was found. In contrast, when pictures were cued with a word, the effect was predominantly distributed over parietal sites. The topgraphical differences suggest that qualitatively distinct processes support successful memory formation in both conditions (Otten & Rugg, 2004). Consistent with these findings, previous ERP studies presenting pictures at both study and test also found frontally distributed subsequent memory effects (Aiqing, Chunyan, Yanhong, Nan, & Jinhong, 2004; Duarte et al.,

2004). Because the functional role of anterior subsequent memory effects has been suggested to relate to semantic processing (Otten et al., 2007), encoding may have emphasised conceptual attributes when memory was later cued with a picture. It may have been easier to rely on conceptual attributes in the picture-picture condition instead of relying on complex perceptual processes. However, the early onset for pictures in comparison to words in the match group suggests that also perceptual processes partly may have played a role.

At first glance it may be counterintuitive that pictures later cued with words show qualitatively different effects than the word-picture condition. In both cases the perceptual overlap between study and test format was reduced relative to the match group. However, the determination whether a presented word was previously encoded as a picture may have required the inspection of the perceptual details of a stored representation only in the picture-word condition. When cued with a word participants may have created a mental image of the object depicted by the word to match the retrieval cue to the encoded picture. To recollect a studied picture, perceptual details of a stored memory representation may have been inspected to decide that the specific object depicted by the word was indeed previously encoded. This is in line with the reports that have been given by participants in the mismatch group. The participants used predominantly a mental imagery strategy when presented with words at test. Thus, pictures later tested with words were most likely remembered when encoding processes emphasised perceptual attributes. In accordance with this interpretation, previous work associated posteriorly distributed subsequent memory effects to visualisation processes (Gonsalves & Paller, 2000) and processing of specific item features and non-semantic encoding tasks (Fabiani et al., 1996; Fernandez, Weyerts, Tendolkar, Smid, Scholz & Heinze,1998; Karis et al.,1984; Otten & Donchin, 2000).

Irrespective of the validity of these interpretations, the findings indicate that encoding-related activity may not only be determined by the physical similarity of the presentation mode, but also by the overlap of functional processes between encoding and retrieval (cf. Roediger, 1990). The dissociation between a frontal versus a posterior subsequent memory effect for pictures in the current experiment may reflect the various engagements of conceptual and perceptual processes as a function of study-test congruency (Blaxton, 1989; Morris et al.,1977). In comparison to words, pictures are more variably processed in terms of conceptual and perceptual attributes (McBride & Dosher, 2002; Mintzner & Snodgrass, 1995; Nelson et al., 1977). In turn, the more features an item contains, the more likely it is that the processes vary between encoding and retrieval (Rajaram 1993; Reingold, 2002; Weldon & Roediger, 1987). It has been shown that the perceptual qualities of images are more distinctive and vary to greater degrees than words (Stenberg et al., 1995) which in turn makes pictures more vulnerable to study-test congruency. This suggests that a deeper understanding of encoding-retrieval overlap could be gained by manipulating the amount of the encoded attributes (e.g. amount of perceptual information) within the same stimulus category.

2.2.1 EXPERIMENT 2: DOES THE AMOUNT OF PERCEPTUAL PROCESSES MODULATE THE STUDY-TEST CONGRUENCY EFFECT AT ENCODING?

Experiment 1 provided support that encoding-related activity varies depending on the degree of study-test congruency. However, this effect was only evident for pictures. While studied pictures later cued with a picture elicited a frontal subsequent memory effect, pictures later probed with a word elicited an ERP effect maximal at posterior electrode sites. In contrast, subsequent memory effects for studied words did not differ as a function of the degree of study-test congruency. Whereas words are predominantly processed in terms of their conceptual attributes, pictures are processed with an emphasis on perceptual and conceptual attributes (McBride & Dosher, 2002; Mintzner & Snodgrass, 1995; Nelson et al., 1977). Stimulus categories that contain more variable features may vary to a greater extent between encoding and retrieval. This in turn leads to stronger encoding-retrieval overlap effects (Reingold, 2002; Rajaram 1993; Weldon & Roediger, 1987). Therefore, a study that manipulates the number of attributes within the same processing type may help to elucidate the functional significance of study-test congruency effects that were evident for pictures. Behavioural studies demonstrated that recognition performance benefits from the amount of perceptual features an item contains. The more perceptual features an item contains, the greater is the overlap between encoding and retrieval (Rajaram, 1996). For instance, images with photographical details lead to better recognition performance than line drawings (e.g. Zannino et al., 2010). Thus, the amount of perceptual information an item contains and the associated perceptual processes may modulate the impact of study-test congruency effects.

Therefore a study that manipulates within the same stimulus category the amount of perceptual processes at encoding and retrieval may elucidate whether the effect of study-test congruency on encoding-related activity is modulated by the amount of attributes an item contains. In order to address this question Experiment 2 varied the emphasis of perceptual processes at encoding and retrieval by manipulating the amount of perceptual information an image contained. Perceptually impoverished images and grey scale photographs were incidentally encoded in a size judgment task. The perceptually impoverished images represented pictures that depicted the contour of objects and animals. The perceptual details within the item were missing

(i.e. outlines). In contrast, the grey scale photographs not only contained the contour of the object, but also the photographic details within the object. At test, half of the encountered outlines and perceptually rich photographs were cued with the same format (photograph-photograph; outline-outline) and half were tested with the alternative format (photograph-outline; outline- photograph).

Congruency in mode of presentation was expected to affect encoding-related brain activity differently as a function of the amount of perceptual information. Photographs contain more perceptual features relative to outlines and therefore may vary to a greater extent as a function of study-test congruency. This was in turn expected to lead to distinct encoding-related ERPs. If the posteriorly distributed effect refers to perceptual processes (e.g. Gonsalves & Paller, 2000), the variation of the amount of perceptual information across study and test was expected to affect the posteriorly distributed subsequent memory effect.

In the specific case of photographs that are later probed with outlines, perceptual analysis processes and the recovery of perceptual details were expected to be evident. Consistent with Experiment 1, the retrieval process may rely on the recollection of those items that were encoded in terms of their perceptual attributes. Therefore, posterior modulations were expected for studied photographs. In contrast, outlines and the underlying brain activity may vary less as a function of study-test congruency. Less perceptual information is incorporated within memory representations and the perceptual processes are thought to vary less between encoding and retrieval. Therefore, it was expected that studied outlines may elicit subsequent memory effects that are less distributed over parietal locations.

2.2.2 METHODS

The EEG acquisition and behavioural data analysis parameters are the same as described in Experiment 1.

PARTICIPANTS

The experimental procedures were approved by the University College London Research Ethics Committee. Nineteen native English speakers were remunerated at £7.50/hour to take part in the experiment (10 women, mean of age 21 years, range 18-27 years). All reported to be right-handed, to have normal or corrected-to-normal vision, and to be free from neurological or psychiatric histories. The data from a further 5 volunteers were excluded from the analysis, because they had fewer than 14 trials due to too good memory performance. All participants provided written informed consent.

STIMULUS MATERIAL

Stimuli were drawn from a pool of 540 photographs of everyday objects and animals (see Figure 7 for examples). Each item was available in the form of a picture and a perceptually impoverished outline. The grey scale photographs were taken from the Hemera Photo Objects suite and were a subset of the pictures used in Experiment 1. Outlines were created by tracing the contour of each photograph by using the Adobe Photoshop software. The outlines were presented in the same dimensions as the corresponding photographs. Three sets of 176 items each were selected pseudorandomly from the pool with the restriction that half of the images in each set consisted of items that in their actual size could fit into a shoebox. The sets were rotated across participants such that each item was presented equally often as a photograph or an outline, and as a studied or unstudied item. Two of the sets were used to create a study list that consisted of 176 outlines and 176 photographs, which were randomly intermixed. All three item sets were used to create a test list of 528 critical items including 176 not yet encountered in the experiment (88 outlines and 88 photographs). At test, half of the studied items were probed in the alternative mode of presentation (outline-photograph; photograph-outline) and the other half in the same mode of presentation (outline-outline; photograph-photograph). Study lists were split into blocks of 88 items and test lists into blocks of 66 items to allow short rest breaks. New random sequences were generated for each participant. The remaining items in the pool were used for practice lists.

EXPERIMENTAL PROCEDURE

The experiment consisted of an incidental encoding task that was followed by a surprise recognition memory test after a half an hour delay (Figure 7). At study, participants saw a series of perceptually impoverished outlines and photographs of objects. Outlines and photographs were equally likely to occur and randomly intermixed. Each outline and photograph was preceded by a cue 'O' or 'P' respectively to indicate whether the upcoming item was an outline or a photograph. In an incidental encoding task, participants had to judge whether or not the presented image could, in its actual size, fit into a shoebox. Participants pressed one of two buttons with their left or right index fingers according to their decision. Both speed and accuracy were stressed. The responding hand was counterbalanced across participants. The study phase started with a short practice list. The study phase was divided in four task blocks. This phase took approximately 25 minutes.

After around 30 minutes, participants were informed that their memory for the items from the shoebox task would be tested. Participants saw a new series of intermixed photographs and outlines that were either studied in the shoebox task or were unstudied (i.e. new). Preceding cues, 'O' or 'P', were again presented before each image to indicate the format of the upcoming image. Half of the studied outlines and photographs were presented in the same mode of presentation as during study (photograph-photograph; outlines-outlines). The other half of the studied outlines and photographs was presented in the alternative mode of presentation (photograph-outline; outline-photograph). All studied outlines and photographs, both in the congruent and incongruent condition, were shown in mirror-reversed orientation as during study (see Figure 7). The change of orientation aimed to remove the possible confounding effects of copy cues in the congruent conditions (Tulving & Pearlstone, 1966). Furthermore, previous studies and pilot work showed that participants relied on stronger memories when orientation was changed between encoding and retrieval (Rajaram, 1996). Participants had to make a 'remember', 'know', or 'new' judgment (Tulving, 1985) by pressing one of three buttons with their right index, middle or ring finger. If participants were confident that they had seen an item before and could recollect specific details from the encoded episode, they had to give a remember response. If they were confident that they had seen the image earlier, but could not recollect any details, a know response had to be made. Finally, if they thought that

the item had not been studied in the shoebox task, they were asked to press the new button. Consistent with Experiment 1, to avoid contamination by guesses, participants also pressed the new button when they were not confident about whether the image was old or new. The participants were instructed to give their memory judgement irrespective of whether an item has been studied as photograph or outline in the shoebox task. The mapping of the response finger to the three different memory decisions was randomised across subjects. Both speed and accuracy were stressed. Before the test phase started, participants familiarised themselves with the task in a practice phase. The test phase was divided in eight task blocks of 66 trials each. The test phase took around one hour.

At study and test, all cues and items were shown in the centre of a computer screen on a white background. The letter cues were presented in red Helvetica font. The cues appeared 1.5 sec before item onset with a visual angle of 0.3 x 0.3° and remained on the screen for 1.4 sec. The screen went blank for the final 100 ms before the item appeared. Photographs and outlines were shown for 1 sec with a visual angle of 1.6 x 1.6°. At study, the time between item offset and the onset of the next cue varied randomly between 1.5 and 3 sec. At test, this time varied between 2.5 and 4 sec. A fixation cross (a plus sign) filled the gaps where no cues and items were presented.

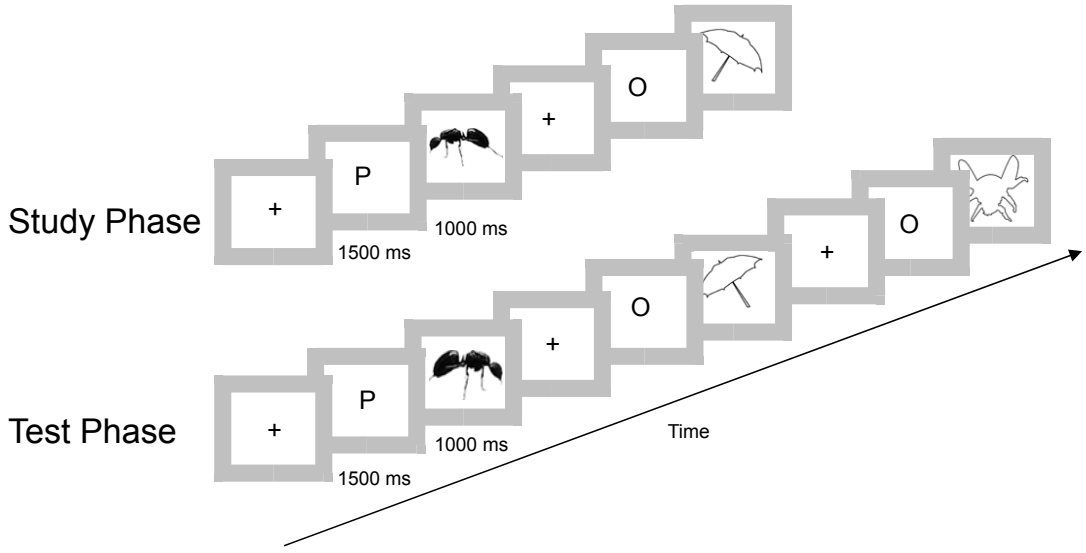

Figure 7. Experimental procedure of study and test phase. Intermixed photographs and outlines were presented at study and test. Cues indicated the upcoming item type. In a R/K recognition test, half of the studied items were presented in the same presentation mode as during study (photograph-outline, outline-photograph) and the other half in the alternative presentation mode (photograph-outline, outline-photograph).

EEG DATA ANALYSIS

The EEG signals were offline digitally filtered between 0.05 and 20 Hz (96 dB roll-off, zero phase shift filter) to remove low- and high-frequency noise. The data were then down sampled to 125 Hz and algebraically re-referenced to averaged mastoids (re-instating the online reference site). For both photographs and outlines, epochs of 2048 ms duration were extracted from the study data starting 100 ms before item onset. The ERP waveforms were created for each subject and each electrode site separately for outlines and photographs in the congruent and incongruent condition by averaging the epochs across all remember trials and across all forgotten trials for each of the four conditions. ERPs were corrected for blink artifacts with a standard regression technique (Rugg et al. 1997). Epochs including drifts exceeding ±50 mV, horizontal eye movements, muscle artifacts and amplifier saturations were excluded from the averaging process. ERPs were based on a minimum of 14 artifact-free trials in each condition. The mean number of remember trials for photographs and outlines in the congruent condition were 25 (14-43) and 32 (19-47). The mean number of forgotten trials for the corresponding conditions were 35 (18-59) and 28 (16-45). The mean number of remember trials and forgotten trials for photographs and outlines in the incongruent condition were 25 (14-46), 33 (14-53), 36 (23-58) and 27 (24-25). Only a subset of participants had at least 14 artifact-free trials for trials associated with know responses (n = 8). Therefore, this response has not been considered in the analyses. The analyses focused on activity elicited by photographs and outlines that were given remember versus new (forgotten) judgments in the subsequent recognition test.

To investigate how study-test congruency and amount of perceptual information affects encoding-related brain activity, subsequent memory effects (Sanquist et al., 1980) were compared across the congruent and incongruent conditions and outline and photograph conditions, respectively. The statistical reliability of amplitude and scalp distribution differences across conditions at encoding was tested by repeated-measures ANOVAs. An initial ANOVA was conducted with the within-subject factors study-test congruency (match/mismatch) and amount of perceptual information (outline/photograph), subsequent memory (remember/ forgotten), and electrode site (32 electrodes, see Figure 3). Follow-up analyses were conducted in case of significant interactions involving subsequent memory to understand the nature of the interactions. Only effects involving subsequent memory are reported.

As already outlined in Experiment 1 for factors with more than two levels, Greenhouse-Geisser corrected *p* values and degrees of freedom are reported to adjust for nonsphericity (Keselman & Rogan, 1980). To establish differences in scalp distributions across conditions, data were scaled with the max/min method to remove overall amplitude differences (McCarthy & Wood, 1985). This procedure has been already described in detail in Experiment 1.

2.2.3 RESULTS

BEHAVIOURAL DATA

ENCODING TASK

Size judgments on outlines in the match condition took on average 768 ms (SD = 130 ms) and 763 ms (SD = 123 ms) in the mismatch condition. For photographs, the RTs were 730 ms (SD = 121 ms) and 738 ms (SD = 114 ms), respectively. An ANOVA contrasting mean response times across overlap and perceptually richness did only reveal a significant main effect of perceptually richness (F (1, 18) = 33.11, $p < .0001$), indicating a longer RT for outlines (765 ms; SD = 29 ms) than photographs (734 ms; SD = 27 ms). Again, accuracy of size judgments was not considered because of the subjective nature of the judgment for many items.

MEMORY TEST

The recognition performance and RT for outlines and photographs in the congruent and incongruent condition are shown in Tables 6, 7 and 8. The ANOVA including recollection- and familiarity-related performance revealed a main effect of study-test congruency (F(1, 18) = 48.29; $p < .0001$, other $p > 0.06$), regardless of the amount of perceptual information (see Tables 6 and 7). Remember responses were generally given more rapidly when items were cued in the same mode of presentation (975 ms, SD = 27 ms) than when probed with incongruent cues (1007 ms, SD = 41 ms). This was true for both outlines and photographs (F(1, 18) = 1245, $p = .002$; other $ps > .123$) (see Table 8).

Table 6. Recollection and familiarity estimates for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N=19).

Study type	Test type	Recollection	Familiarity
Photograph	Photograph	0.40 (0.13)	0.25 (0.16)
	Outline	0.26 (0.07)	0.16 (0.12)
Outline	Outline	0.36 (0.08)	0.24 (0.14)
	Photograph	0.28 (0.10)	0.17 (0.11)

Values are across-subject means (SD).

Table 7. Mean proportion of remember, know, new responses for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N=19).

Study type	Test type	Remember	Know	New
Photograph	Photograph	0.46 (0.12)	0.20 (0.11)	0.34 (0.12)
	Outline	0.31 (0.09)	0.20 (0.10)	0.49 (0.15)
Outline	Outline	0.42 (0.10)	0.23 (0.12)	0.35 (0.09)
	Photograph	0.33 (0.11)	0.20 (0.12)	0.47 (0.10)
New	Photograph	0.05 (0.04)	0.12 (0.08)	0.83 (0.08)
	Outline	0.05 (0.04)	0.14 (0.09)	0.81 (0.09)

Values are across-subject means (SD).

Table 8. Mean RT of remember, know, new responses for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N=19).

Study type	Test type	Remember	Know	New
Photograph	Photograph	988 (158)	1160 (390)	1039 (261)
	Outline	531 (514)	1090(799)	1044 (239)
Outline	Outline	988 (158)	1195 (309)	1050(249)
	Photograph	996 (182)	1254 (371)	1024 (234)
New	Photograph	1013 (187)	1253 (321)	995 (214)
	Outline	880 (469)	1160 (442)	1035 (244)

Values are across-subject means (SD).

EVENT-RELATED POTENTIALS

The grand averaged ERP waveforms for studied outlines and photographs that were subsequently cued in the congruent and incongruent presentation mode are shown in Figure 8. ERPs elicited by remembered outlines and photographs in the congruent and incongruent conditions were more positive-going than when they were later forgotten. At the beginning of the epoch, this effect was pronounced over frontal electrode sites for outlines and photographs irrespective of study-test congruency. However, approximately 700 ms post stimulus the subsequent memory effect was more widespread and pronounced over posterior sites for outlines and photographs cued with incongruent retrieval probes. In contrast, studied pictures and outlines cued with congruent probes elicited positive-going modulations over frontal electrodes (see Figure 9 and Figure 10 for spline maps). Statistical analyses confirmed these observations. The chosen time regions captured the largest subsequent memory effects and possible changes over time. Consistent with Experiment 1 repeated measures ANOVAs on mean amplitudes were conducted separately for three time windows: 100-700 ms, 700-1300 ms, 1300-1900 ms.

In the early time window the analysis revealed a significant interaction between study-test congruency and subsequent memory ($F(1,18) = 5.50$, $p = .031$), indicating a greater subsequent memory effect for items in the incongruent ($M = 0.77$ μV) than congruent condition ($M = 0.08$ μV). Moreover, the analysis revealed a significant main effect of subsequent memory ($F(1,18) = 7.91$, $p = .012$) and an interaction with site ($F(4.2, 75.5) = 12.10$, $p < .0001$). Consistent with experiment 1, subsidiary analyses on five frontal (sites 21, 34, 35, 36, and 50) and five parietal electrodes (sites 12, 14, 16, 26, 29) were conducted to understand the nature of the interaction. A subsequent analyses on five frontal electrodes revealed a significant subsequent memory effect ($F(1,18) = 24.18$, $p < .0001$). In contrast the analysis on five parietal electrodes did not result in a significant subsequent memory effect ($p = .867$). These findings indicate that the subsequent memory effect was pronounced over frontal electrode sites within the early latency region irrespective of item type and study-test congruency (see Tables 9 and 10).

In contrast to the early time window, the analyses for the data between 700 and 1300 ms revealed a significant interaction between study-test congruency, subsequent memory and site ($F(3.2,56.8) = 3.03$, $p = .035$). The subsidiary analysis for the congruent condition resulted in a significant interaction between subsequent memory ($F(1,18) = 8.63$, $p = .009$) and site ($F(2.8,50.1) = 6.64$, $p = .001$). Consistent with Experiment 1, follow-up analyses with five frontal and five parietal electrodes were conducted. The analyses incorporating five frontal sites revealed a significant main effect of subsequent memory ($F(1,18) = 12.94$; $p = .002$; other ps $> .242$), indicating a frontally distributed subsequent memory effect for the congruent condition. The analyses for the incongruent condition resulted also in a significant main effect of subsequent memory ($F(1,18) = 45.93$, $p < .0001$) and an interaction with site ($F(3.6,64.6) = 5.47$, $p = .001$). Follow-up analyses on five frontal and five parietal electrodes revealed significant main effects of subsequent memory for both frontal ($F(1,18) = 45.23$, $p < .0001$) and parietal sites ($F(1,18) = 34.22$; $p < .0001$), suggesting a widely distributed subsequent memory effect for the incongruent condition (see Tables 9 and 10). The analysis on the scaled data confirmed the findings in the second latency region. The analysis on the scaled data across all 32 electrodes revealed a significant interaction between study-test congruency and electrode site ($F(3,9,6.2) = 2.48$, $p = .035$). The analyses on the scaled data for the congruent condition and

incongruent condition revealed also a significant interaction with site (F(2.8,50.3) = 6.63, p = .001; F(3.5,63.7) = 4.07, p = .007).

The analysis for the data between 1300ms and 1900ms resembled the findings in the middle latency region. The ANOVA resulted in a significant interaction between study-test congruency, subsequent memory and site (F(3.7, 66.9) = 3.22, p = .020). Subsidiary analyses for the congruent condition revealed a significant interaction between subsequent memory and site (F(3.0,54.7) = 3.95, p = .012). Follow-up analyses on five frontal and posterior electrodes resulted in a significant interaction between subsequent memory and sites only over frontal locations (F(2.0,36.0) = 3.76, p = .033; other ps > .227). For the incongruent condition the analyses revealed a main effect of subsequent memory (F(1,18) = 4.60, p = .046), indicating a widely distributed subsequent memory effect for the incongruent condition (see Table 9 and 10). The analyses on the scaled data across all 32 electrode sites resulted in a significant interaction between study-test congruency and electrode sites (F(3.96, 71.19) = 2.54, p = .048). The subsidiary analyses revealed also a significant interaction with site for the congruent condition (F(3.2,57.9) = 3.60, p = .016).

Subsidiary analyses including the three time intervals as an additional factor confirmed the observed topographical modulations as a function of study-test congruency over time. An ANOVA revealed a significant interaction between interval, study-test congruency, subsequent memory and electrode site (F(6.2,111.5) = 36.35, p = .002). This analyses remained significant after scaling the data (F(6.1,109.9) = 2.32, p = .037). The same pattern of results was observed for the subsidiary comparison between the first and second and first and last interval (F(4.7,83.8) = 4.82, p = .001; F(4.6,83.2) = 4.23, p = .002). Both interactions remained significant after scaling the data (F(4.1,74.1) = 2.69, p = .036; F(4.8,86.5) = 2.68, p =.029). In contrast, the comparison between the second and the third time interval did not reveal a significant interaction between interval, study-test congruency, subsequent memory and site (p = .474), indicating topographical differences only between the first and the last two time intervals.

In sum, encoding-related activity did not vary with the amount of pictorial information. Irrespective of the study-test congruency and the amount of pictorial information, the subsequent memory effect was pronounced over anterior electrodes in the early latency region. However, encoding-related brain activity did differ in its amplitude depending on the degree of study-test congruency in the first latency region. Items that were later cued in the alternative presentation mode showed a stronger effect than when cued with congruent probes. In comparison to the early latency region, encoding-related ERPs differed qualitatively as a function of study-test congruency in the last two latency regions. While items that were probed with a congruent cue elicited frontally distributed subsequent memory effects, the subsequent memory effect for items probed with incongruent cues was more widespread in the middle latency region and last time region.

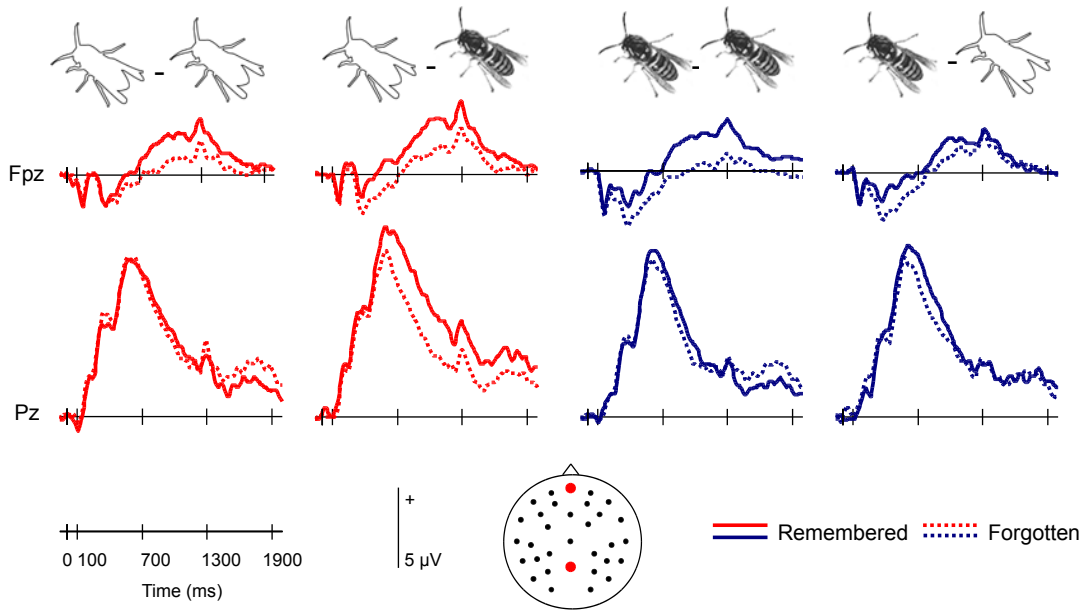

Figure 8. Encoding-related neural activity. Group averaged ERP waveforms at study are compared for later remembered (solid line) versus forgotten (dotted line) outlines (highlighted in red) and photographs (highlighted in blue) in the congruent and incongruent condition. The waveforms for two representative midline electrode sites (equivalent to Fpz and Pz of the international 10/10 system) are displayed. Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes.

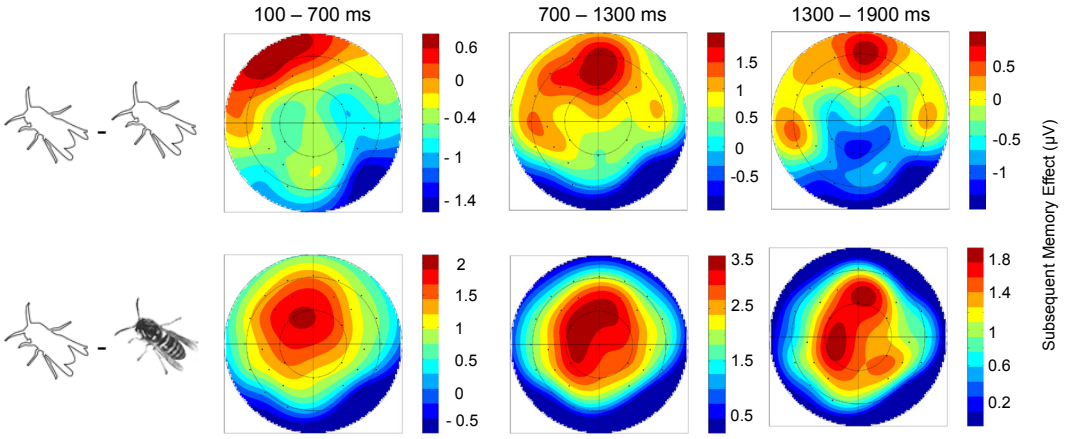

Figure 9. The spline maps illustrate the scalp distribution of the difference activity between subsequently remembered and forgotten outlines cued with an outline (top) and probed with a photograph (bottom) in the latency region of 100-700 ms, 700-1300 ms and 1300-1900 ms.

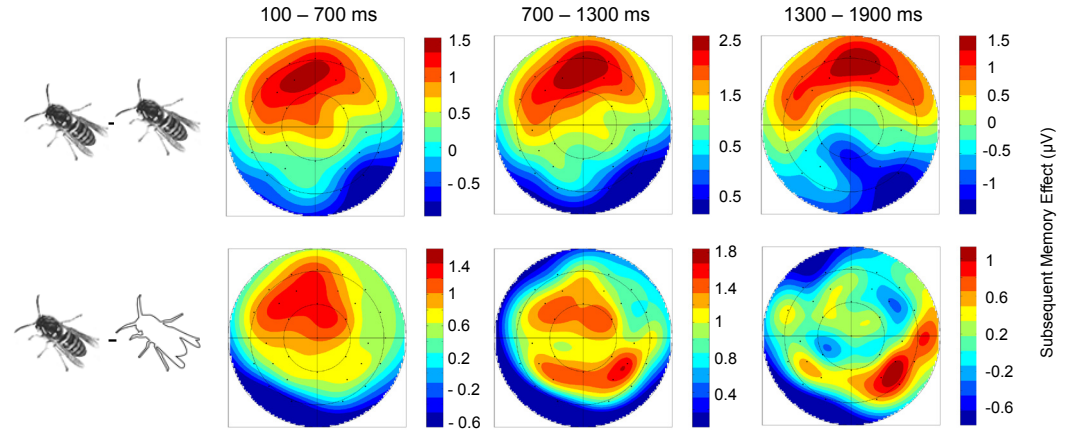

Figure 10. Scalp distributions of the ERP difference between later remembered and forgotten photographs later cued with a photograph (top) and subsequently probed with an outline (bottom) in the three latency regions.

Table 9. F statistics and *p* values of key effects in the global ANOVAs on electrical brain activity.

	Latency Interval		
Effect	100-700	700-1300	1300-1900
MA x SM x ST	$F(2.7,49.1) = 1.49$, $p = .232$	$F(3.2,56.8) = 3.03$, $p = .035$*	$F(3.7, 66.9) = 3.22$, $p = .020$*

Degrees of freedom and *p* values are Greenhouse-Geisser corrected. MA = study-test congruency; SM = subsequent memory; ST = electrode site. * = significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985).

Table 10. F statistics and *p* values of the key effects in the follow-up within-group ANOVAs in the congruent and incongruent condition.

		Latency Interval	
Group	Effect	700-1300	1300-1900
Match	SM x ST	$F(2.8,50.1) = 6.64$, $p = .001$*	$F(3.0,54.7) = 3.95$; $p = .012$*
	SM anterior sites	$F(1,18) = 12.94$; $p = .002$	$F(2.0,36.0) = 3.76$; $p = .033$
	SM posterior sites	$F(1,18) = 1.47$; $p = .242$	$F(1,18) = 1.57$; $p = .227$
Mismatch	SM x ST	$F(3.6,64.6) = 5.47$; $p = .001$*	$F(3.8,69.1) = 0.83$; $p = .502$
	SM anterior sites	$F(1,18) = 45.23$; $p < .0001$	– – –
	SM posterior sites	$F(1,18) = 34.22$; $p < .0001$	– – –

Degrees of freedom and *p* values are Greenhouse-Geisser corrected. SM = subsequent memory; ST = electrode site; --- = no follow-up analyses were conducted due to non-significant interaction with site; * = significant after scaling the data to remove overall amplitude differences between conditions (McCarthy & Wood, 1985). Anterior sites refer to the five most frontal electrodes in the montage (sites 21, 34, 35, 36, and 50 of montage 10 at http://www.easycap.de/easycap/e/electrodes/13_M10.htm). Posterior sites refer to five equivalent parietal ones (sites 12, 14, 16, 26, 29).) and parietal sites

2.2.4 DISCUSSION

Experiment 2 investigated whether encoding-related ERPs vary depending on the amount of perceptual processes and the degree of similarity of these operations across encoding and retrieval. This question was addressed by presenting perceptually impoverished outlines and grey scale photographs at study. At test, half of the items were presented in the same presentation mode at study and half in the alternative mode.

The behavioural findings provide strong support for the study-test congruency effect. RT for remembered responses and overall memory performance showed an advantage for images later cued in the congruent presentation mode irrespective of the amount of perceptual information. The behavioural findings are in line with the behavioural findings in Experiment 1 and with previous studies demonstrating that memory benefits from an overlap between study and test processes (Jacoby, 1996; Hornberger et al., 2004; Mulligan & Osborn, 2009; Stenberg et al., 1995; Schloerscheidt & Rugg, 2004; Park & Rugg, 2008).

In line with the behavioural performance, Experiment 1 and neuroimaging findings (Park & Rugg, 2008), encoding-related brain activity differed qualitatively depending on the study-test congruency. While images that were later tested in the congruent presentation mode elicited a subsequent memory effect over frontal scalp sites, the subsequent memory effect for items later tested with incongruent probes was distributed over posterior scalp locations. However, unexpectedly the amount of pictorial information at study and test did not have an influence on the subsequent memory effect.

Interestingly, the topographical modulation as a function of study-test congruency did not emerge immediately after item onset, but started around 700 ms post stimulus. Directly after item onset, amplitude differences were evident as a function of study-test congruency. The subsequent memory effect for items later probed in an alternative presentation mode was significantly larger, suggesting more involvement of similar cognitive processes for the mismatch condition irrespective of the amount of perceptual information. These subsequent memory effects were most pronounced over frontal sites which have been associated with semantic or associative encoding processes in the previous literature (see for review Johnson & Friedman, 2000; Otten et al., 2007; Weyerts et al., 1997). At first glance, it might

be counterintuitive that mismatch conditions elicited a stronger frontal subsequent memory effect, because items in the match conditions were remembered to a greater extent. However, encoding-related activity most probably reflects these encoding processes that are used for later successful memory retrieval. One could suggest that participants remembered especially those items in the mismatch condition that were encoded with a stronger emphasis on semantic processes. In contrast, in the match condition less effort of semantic encoding strategies may have already been sufficient to remember the item successfully, because retrieval was overall easier in the match condition. Alternatively, encoding-related activity refers to qualitatively different processes as a function of study-test congruency in the first time region, but because of low statistical power these differences were not statistically reliable (Otten & Rugg, 2004).

Consistent with Experiment 1, additional posterior contributions were only observed for the mismatch condition approximately in the middle of the analysis epoch. Considering previous findings, the posterior effects may reflect perceptual processes (Gonsalves & Paller, 2000; Otten & Donchin, 2000; Fernandez et al., 1998). Consistent with Experiment 1, additional perceptual inspections might have been engaged in the mismatch condition at retrieval to decide confidently that the specific image was indeed initially encountered in the alternative format. Therefore, participants most probably remembered those items that were encountered with a greater emphasis on perceptual details.

However, the effect in the mismatch condition in the Experiment 2 was more widespread and was also pronounced over frontal locations. How do the findings relate to Experiment 1? The differences in the experimental designs between both experiments might explain the distribution differences. In Experiment 1 study-test congruency was manipulated between subjects. Therefore, participants in the mismatch group may have prepared for the upcoming test probe more specifically when preceding cues were shown at test. For instance, when a word cue ('W') appeared at test participants in the mismatch group could anticipate that the studied item was presented as a picture and vice versa. Therefore, a specific strategy, most likely oriented to perceptual attributes, could have been engaged in the picture-word condition. The retrieval orientation data in Experiment 1 (see Appendix 1) confirm this interpretation. Already before the test cue was presented, at the time when the letter cue was shown, ERP waveforms differed significantly according to the study-test congruency and the amount of perceptual information.

In Experiment 2, photographs and outlines that were congruent or incongruent to the studied presentation mode were presented intermixed at test. Here, participants could not possibly engage a specific 'retrieval orientation' supporting the search for memory representations that match or mismatch with the presentation mode of the test probe. Therefore, the retrieval cues, 'P' and 'O', were not informative in terms of the studied presentation mode and in turn participants could not establish a specific retrieval focus for a particular stimulus type. For instance, an outline cue might have been initially encountered as outline (match) or as photograph (mismatch) and vice versa. Thus, it might have been most beneficial to be focused overall on conceptual attributes which would be evident in a frontally distributed effect irrespective of the study-test congruency of the presentation mode. However, in the mismatch conditions it would have been additionally of benefit to subsequently engage perceptual analysis processes beside conceptual processes to ensure that indeed the specific image was shown in the alternative format at study. This may have been evident in additional posterior contributions for the mismatch conditions. Therefore, the widespread subsequent memory effect elicited by images later cued with incongruent probes reflects most likely emphasis on both conceptual and perceptual attributes.

Crucially, the effect of study-test congruency was not modulated by the amount of perceptual information, but appeared to be evident for images in general (i.e. outlines and photographs). These findings suggest that images with respect to specific perceptual attributes are incorporated in memory representations, because study-test congruency influenced the encoding-related activity for outlines and photographs. However, the type of process that supports an episodic memory trace does not differ depending on the amount of perceptual information. Thus, encoding-retrieval overlap plays a role for the encoding-related activity for images in general. As discussed in Experiment 1, images generally are processed with a greater emphasis of their conceptual and perceptual attributes (McBride & Dosher, 2002; Mintzner & Snodgrass, 1995; Nelson et al., 1977) than for instance words. The various contributions of both conceptual and perceptual processes make images possibly more sensitive to the study-test congruency manipulation.

Experiment 2 demonstrated that the degree of study-test overlap affects the neural correlates of episodic encoding of images irrespective of the amount of perceptual information. Considering the findings from Experiment 1 and Experiment 2, the impact of encoding-retrieval overlap on the neural correlates of encoding may be specific to events that are characterised by perceptual as well as conceptual processes, such as images. Future research that explicitly manipulates the emphasis on perceptual and conceptual processes at retrieval might reproduce the pattern of results and uncover the functional significance of the dissociation between frontal and posterior distributions of subsequent memory effects.

2.3.1 EXPERIMENT 3: THE INFLUENCE OF CONCEPTUAL AND PERCEPTUAL TEST PROBES ON ENCODING-RELATED BRAIN ACTIVITY

Experiment 3 investigated how neural correlates of encoding vary as a function of the type of retrieval processes. The transfer-appropriate processing framework stresses that memory retrieval benefits from both perceptual and conceptual processes and it is the appropriate interaction of these processes between encoding and retrieval that determines whether we remember an event or not (Roediger et al., 2002). Therefore, Experiment 3 aimed to elucidate whether encoding-related activity differs qualitatively depending on whether retrieval emphasises perceptual or conceptual processes. This research question emerged directly from the findings from the first and second study that will be briefly reviewed in this introduction.

There is initial evidence, that encoding-related activity varies depending on how memory is subsequently probed (Bridger & Wilding, 2010; Otten, 2007; Park & Rugg, 2008). For instance, a recent ERP study showed evidence that encoding-related brain activity varies qualitatively depending on the type of retrieval requirements (Bridger & Wilding, 2010). Words that were presented at the left or right site of fixation were encoded in two different encoding tasks. Across different test blocks, participants were either required to remember the screen location or the type of encoding task. Qualitatively different brain activities were associated with encoding success as a function of the retrieval focus. While the subsequent memory effect for the type of encoding task was positive-going and frontally distributed, the subsequent memory effect related to the retrieval of the location information was reversed in polarity. This study provides initial evidence that encoding-related ERPs vary with the type of retrieved information. Moreover, Experiment 1 and 2 suggest that encoding-related activity varies qualitatively with the functional overlap between encoding and retrieval processes. While encoding-retrieval overlap was associated with frontal subsequent memory effects, perceptual mismatch was associated with posteriorly distributed encoding-related activity. Together, the previous findings indicate that the specific retrieval focus affects the neural correlates of encoding (Bridger & Wilding, 2010).

A study that isolates conceptual from perceptual retrieval processes may elucidate whether the distinction in those two processes is indeed associated with

frontally and posteriorly distributed subsequent memory respectively. Therefore, in Experiment 3 encoding-related activity was compared across test probes that emphasised perceptual or conceptual processes. Electrical brain activity was recorded while participants made size judgments on photographs of objects. In a later memory test, half of the objects were probed with the same photograph as presented at study and half with another exemplar that depicted the same kind of object or animal respectively. On each test trial, participants were cued to either make an exclusion judgment ("do you remember seeing this photograph?") or an inclusion judgment ("do you remember seeing this object").

Jacoby et al. (1993) introduced initially this type of memory test to differentiate between different types of recognition memories. The exclusion task refers to a 'specific' retrieval focus. In the context of the present study participants had to accept the presented images only as old if the exact image including all perceptual features was shown in the study phase. Unstudied items and exemplars of the same category had to be rejected as new. In contrast, in the inclusion task participants had a general or conceptual focus, because the identical cues (i.e. copy cues) and exemplars of the same category that were initially studied had to be accepted as old. Only unstudied items that depicted a different category as the ones initially studied had to be rejected as new. The exclusion task is thought to rely on perceptual processes, because participants most likely need to rely on the recollection of the perceptual details of the image to correctly accept the items as old. In contrast, the latter task is thought to emphasise especially conceptual processes. Items had to be accepted as old as long as the same category initially has been studied; regardless of the physical similarity of the images (Ecker & Zimmer, 2009; Ranganath, Johnson & D'Esposito, 2000). Consistent with the transfer-appropriate processing framework, it was expected that images that were encoded with an emphasis on conceptual attributes were most likely remembered in the inclusion task. On this account, encoding-related activity was expected to reflect most likely conceptual processes, because these processes overlapped with the processes emphasised in the inclusion task. Based on the ERP findings in Experiment 1 and 2 and studies that investigated semantic processes at study (Johnson & Friedman, 2000; Otten et al., 2007; Weyerts et al., 1997), it was predicted that a more frontally distributed subsequent memory effect would be evident for studied pictures that were remembered in the conceptual task (i.e. inclusion task).

In contrast, images that were later tested in the exclusion task were thought to be remembered best when the images were initially encoded with an emphasis on their perceptual attributes. On this account, encoding-related activity for images later tested in the exclusion task was thought to reflect most likely perceptual encoding processes. Therefore, it was expected that pictures successfully remembered in the picture task (i.e. exclusion task) are associated with a subsequent memory effect with its maximum over posterior sites (e.g. Gonsalves & Paller, 2000; Fernandez et al., 1998; Otten & Donchin, 2000).

2.3.2 METHODS

The EEG acquisition parameters and procedure was the same as outlined in Experiment 1.

PARTICIPANTS

The experimental procedures were approved by the University College London Research Ethics Committee. Subjects were right-handed and native English speakers as assessed by self-report. The analyses are based on the data of 24 subjects (mean age: 22 years; age range: 19-30; 12 female). The data from a further four volunteers were excluded due to electrooculogram (EOG) artefacts (n = 2) and insufficient numbers of trials because of extreme high or low memory performance (n = 2). All participants gave written informed consent and were paid £ 7.50/hour for participation. All of them reported to have normal or corrected-to-normal vision and no neurological and psychiatric histories.

STIMULUS MATERIAL

Stimuli were drawn from a pool of 530 black-and-white pictures of everyday objects (e.g. tools) and animals. Each item was available in the form of two kinds of exemplars that differed in their perceptual features on different dimensions (e.g. orientation, shade). Approximately half of the stimuli were the same as used in Experiment 2. Six sets of 86 pictures were selected pseudo-randomly. Half of the pictures in each set could fit in a shoebox – in real size- and the other half of objects were bigger than a

shoebox. The lists were rotated such that each item was presented equally often during the study phase and as an unstudied picture during the test phase.

At study, participants saw 344 pictures randomly intermixed. Test lists contained all studied items and 172 unstudied pictures (in total 516 items). In both, 'Concept' and 'Picture' condition, half of the studied pictures were perceptually identical and half of the studied items were cued by exemplars that depicted the same kind of thing as during study, but contained different perceptual features (see Figure 11). The remaining items in the stimulus pool were used for practice lists. New random sequences were generated for each participant.

PROCEDURE

The experiment consisted of an incidental encoding phase and a surprise recognition memory test after 30 minutes delay (see Figure 11). At study, participants saw randomly intermixed pictures on the computer screen. Exclamation marks were presented 500 ms before stimulus onset to warn the participant of the upcoming item. Trials were separated by a fixation cross (+). By pressing one of two buttons participants decided whether or not the presented object would fit in a shoebox – in its real size. They were instructed to respond as quickly and as accurately as possible with their left or right index fingers depending on their decision. The responding hand was randomised across the participants. A short practise list was given prior to the study phase. The study phase was split into four blocks of 86 trials each. The blocks were separated by rest periods. The study phase took approximately 25 minutes.

The test phase followed the study phase after approximately 30 minutes. At this point, volunteers found out that their memory would be tested. All studied items (half same pictures and half exemplars) were presented again, intermixed with unstudied items. During test, participants were instructed to flexibly switch between two kinds of judgements. Verbal cues ('Concept' or 'Picture') started 1.5 sec before each test item and indicated which type of judgement participants had to make on the upcoming image. The cues were presented below each picture and remained on the screen until the picture disappeared. Volunteers were instructed to attend the cues to identify the task instruction for the upcoming item. In the 'Picture' condition participants were instructed to be focused on the perceptual features of the test cue and only accept them as old if they were confident that the picture was identical in its perceptual features to the image presented at study. In contrast, in the 'Concept'

condition, participants accepted the items as old if they were confident that the picture depicted the same kind of object irrespective of whether it was perceptually modified or not. To avoid contamination by lucky guesses, participants also pressed the new button when they were not confident about their decision.

The mapping of the responding hands and corresponding decisions was randomised across subjects. Again, both accuracy and speed were stressed. A practise block preceded the test phase. The test phase was split into eight blocks and was around 80 minutes in length. At both study and test, all critical items were presented in central vision on a white background for 1 s and were shown with an approximate visual angles of 1.6 x 1.6°. A black Helvetica font was used for the verbal cues at test. At study, the time between item offset and the onset of the next cue varied randomly between 1.5 and 3 sec. At test, this time varied between 2.5 and 4 sec.

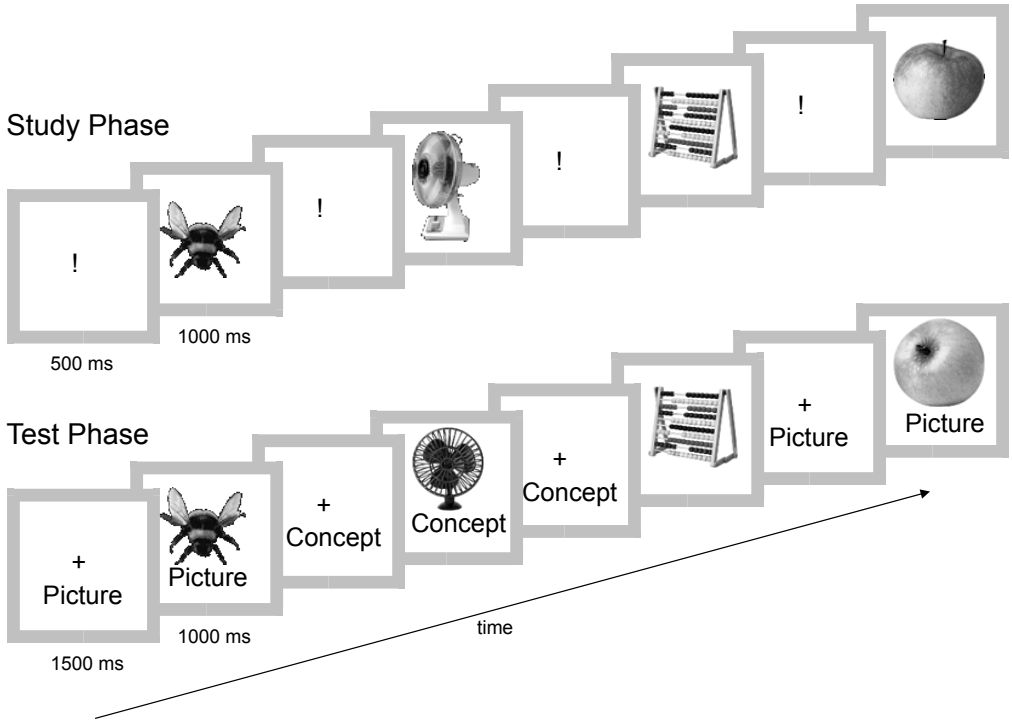

Figure 11. Experimental procedure of study and test phase. A series of photographs were presented at study in an incidental encoding task (size judgement task). At test in an old/new recognition task, half of the studied photographs were cued with exactly the same image (copy cues) and half were probed with an exemplar of the same category. Verbal cues at test indicated the retrieval judgement for the upcoming photograph. The cue 'Concept' indicated that the participants had to judge whether they could remember the object from the study phase irrespective of whether it was a copy cue or an exemplar. The cue 'Picture' indicated that the participants had to accept the upcoming picture as old only if it was a copy cue of the image shown at study.

BEHAVIOURAL DATA ANALYSIS

'Pr' (Snodgrass & Corwin, 1988) was used to assess memory accuracy and compare memory performance across the retrieval types by subtracting the proportion of false alarms (new items incorrectly judged as old) from the proportion of hits (old items correctly judged as old). To investigate differences in false alarms across the conditions 'Br' (Snodgrass & Corwin, 1988) was calculated to assess the response bias for the different conditions by dividing the proportion of false alarms by (1 – Pr).

EEG DATA ANALYSIS

Signals were offline digitally filtered between 0.05 and 20 Hz (96 dB roll-off), down sampled to 125 Hz, and algebraically re-referenced to averaged mastoids (re-instating the online reference site). The length of the EEG epoch for the study extended from 100ms before an item to 1948 ms after item onset. The ERP waveforms were created for each subject and each electrode site separately for pictures that were tested in the 'Concept' and 'Picture' conditions. Epochs with drifts exceeding ±50 mV, horizontal eye movements, muscle artifacts or amplifier saturations were excluded from the averaging process. Averaged ERPs in each condition were based on a minimum of 14 artifact-free trials. The mean number of trials (range in brackets) for subsequently recognized responses for copy cues in the 'Picture' task, in the 'Concept' task and for exemplars in the 'Concept' task were 35 (18-64), 48 (25-67) and 36 (21-57). The mean number of trials of the later forgotten responses for the corresponding conditions were 37 (15-57), 24 (14-46) and 36 (15-57).

In order to identify differences in neural activity according to the type of retrieval process, again the timing, scalp distribution and amplitude of ERP effects at encoding was considered. To investigate how the ERPs during encoding varied according to the type of retrieval processes, the subsequent memory effect (i.e. old vs. forgotten) was compared for those pictures that were subsequently cued with the copy cue at test in the 'Picture' and 'Concept' condition. Moreover, the subsequent memory effect for exemplars in the 'Concept' condition were statistically analysed and compared with the ERPs associated with copy cues in the 'Concept' condition. Although this was not the main focus of this study, this comparison would elucidate whether similar qualitative dissociations as a function of study-test congruency would emerge as in Experiments 1 and 2.

Initial repeated measures ANOVAs incorporated the within-subject factors retrieval condition (copy in 'Picture' task, copy cue in 'Concept' task, exemplar in 'Concept' task), subsequent memory (old vs. forgotten), and electrode site (see Figure 3). Statistical comparisons of the mean amplitude on the items that were cued with copy cues incorporated the within subject factors retrieval process (conceptual vs. perceptual), subsequent memory (old vs. forgotten), and electrode site (see Figure 3). In case of significant interactions involving subsequent memory follow up analyses were conducted to understand the nature of the interactions.

Again, where necessary (i.e. factors with more than 2 levels) the reported p-values and degrees of freedom (dfs) refer to Greenhouse-Geisser corrected values for non-sphericity (Keselman and Rogan, 1980). In case of scalp topography differences statistical comparisons were conducted on the scaled data (McCarthy & Wood, 1989). For detailed information regarding the scaling procedure see Experiment 1.

2.3.3 RESULTS

BEHAVIOURAL DATA

ENCODING TASK

Size judgments on pictures that were subsequently cued with the identical image in the 'Picture' condition and the 'Concept' condition took on average 784 ms (SD = 129 ms) and 786 ms (SD = 153 ms) respectively. For pictures in the 'Concept' condition that were subsequently cued with an exemplar (mismatch condition), the reaction time was 776 ms (SD = 128 ms). An ANOVA contrasting mean response times across these three retrieval conditions did not reveal significant differences (p = .570). Accuracy of size judgments was not considered because of the subjective nature of the size judgement

MEMORY TEST

Recognition memory performance and RT are listed in Table 11 and Table 12. For identical test cues, Pr was 0.42 and 0.44 in the 'Picture' and 'Concept' condition, respectively. For exemplars in the 'Concept' condition Pr was 0.28. A repeated measures ANOVA incorporating the three retrieval conditions revealed a significant main effect ($F(1.6,37.5) = 44.76$, $p < .0001$). A paired sample t-test on the Pr for copy cues between the 'Concept' and 'Picture' condition gave rise to a significant retrieval task effect ($t(23) = -2.20$, $p = .038$). Moreover, a paired sample t-test on the Pr between the identical and exemplar condition in the 'Concept' condition revealed also a significant effect ($t(23) = 9.32$, $p < .001$). The comparison between the 'Picture' condition and the 'Concept' condition with mismatch cues (i.e. exemplars) was also significant ($t(23) = 5.97$, $p < .0001$). Response bias was significantly higher in the 'Concept' condition (Br of 0.41) than in the 'Picture' condition (Br of 0.14) for copy cues ($t(23) = -10.04$, $p < .001$). Moreover, the response criterion was more liberal for identical test cues than for exemplars (Br of 0.32) in the 'Concept' condition ($t(23) = 8.25$, $p < .001$).

Correct old responses were given quicker for copy cues than for exemplar pictures in the 'Concept' condition ($t(23) = -5.63$, $p < .001$) (see Table 12). The reaction time for correct old responses for pictures later cued in the congruent presentation probe did not differ between the 'Concept' and 'Picture' condition ($p = .599$).

Table 11. Recognition performance for copy cues and exemplars in the 'Concept' and 'Picture' task (N=24).

Task	Item type	Old	New
Picture	Old identical	0.50 (0.13)	0.50 (0.14)
	Old exemplar	0.24 (0.08)	0.76 (0.08)
	New picture	0.08 (0.05)	0.92 (0.05)
Concept	Old identical	0.67 (0.11)	0.33 (0.11)
	Old exemplar	0.51 (0.13)	0.49 (0.13)
	New Picture	0.23 (0.09)	0.77 (0.09)

Values are across-subject means (SD).

Table 12. Mean RTs (ms) for copy cues and exemplars in the 'Concept' and 'Picture' task (N=24).

Task	Item type	Old	New
Picture	Old identical	1104 (293)	1169 (312)
	Old exemplar	1165 (316)	1146 (294)
	New picture	1216 (322)	1099 (268)
Concept	Old identical	1118 (265)	1218 (333)
	Old exemplar	1189 (290)	1191 (321)
	New Picture	1271 (302)	1156 (314)

Values are across-subject means (SD).

EVENT-RELATED POTENTIALS

Group averaged ERPs elicited by later remembered and forgotten responses for pictures that were probed with copy cues and exemplars in the 'Concept' conditions and with copy cues in the 'Picture' condition are shown in Figure 12. ERPs associated with exemplars in the 'Picture' task are not considered, because these items had to be rejected as new. ERPs elicited by images that were associated with an old judgement in the 'Picture' task were more positive-going than later forgotten pictures. This subsequent memory effect was pronounced over central and centro-parietal electrode sites at the beginning of the analysis epoch and shifted to frontocentral locations after around 800 ms. In contrast, the subsequent memory effect associated with items tested with identical pictures in the 'Concept' condition was less sustained until approximately 900 ms of the epoch and was smaller in amplitude and distributed over only frontocentral sites. The subsequent memory ERP effect for pictures later cued with exemplars in the 'Concept' condition was widely distributed (see Figure 13).

Repeated measures ANOVA on mean amplitudes were conducted separately for an early and a late latency region (500-900 ms and 900-1300 ms). An earlier and a later latency region were selected based on visual inspection of the largest subsequent memory effects of group averaged ERPs to statistically test whether this effect would be consistent across subjects (see figure).

Within the early time window, the initial analysis incorporating the retrieval condition (Concept exemplar/Concept same/Picture same), subsequent memory (confident old/forgotten) and sites (all 32 sites) did not reveal a significant interaction with retrieval type (p = .210). The analyses resulted in a main effect of subsequent memory (F(1,23) = 31.24, p < .0001) and an interaction with site (F(3.3, 76.6) = 5.69, p = .001; see Figure 13).

In contrast, within the later latency region the initial analyses incorporating all three conditions revealed a significant interaction between retrieval condition and subsequent memory (F(2.0,45.2) = 4.26, p = .021). Subsidiary analyses were conducted between pairs of retrieval conditions to understand the nature of the interaction. The analyses comparing the effects associated with copy cues in the 'Concept' and 'Picture' conditions revealed a significant interaction between retrieval condition and subsequent memory (F(1,23) = 4.84, p = .038). Moreover, the comparison between copy cues and exemplars in the 'Concept' task revealed also a significant interaction between retrieval condition and subsequent memory (F(1,23) = 8.66, p = .007). Interestingly, the comparison between copy cues in the 'Picture' task and exemplars in the 'Concept' task did not reveal differences (p > .335).

Across both conditions, the analyses resulted in a significant main effect of subsequent memory (F(1,23) = 13.21, p = .001) and an interaction with site (F(4.0,91.4) = 4.42; p = .003). Follow-up analyses on the copy cues in the 'Concept' task did not reveal a significant subsequent memory effect (p > .346).

In sum, the subsequent memory effect differed in its amplitude as a function of the retrieval condition. This was only evident between 900 and 1300 ms. The 'Concept' and 'Picture' retrieval focus were not associated with distinct subsequent memory effects. While the 'Concept' condition with exemplars (mismatch) and the 'Picture' condition elicited widespread subsequent memory effects, the subsequent memory effect for copy cues in the 'Concept' condition was not significant.

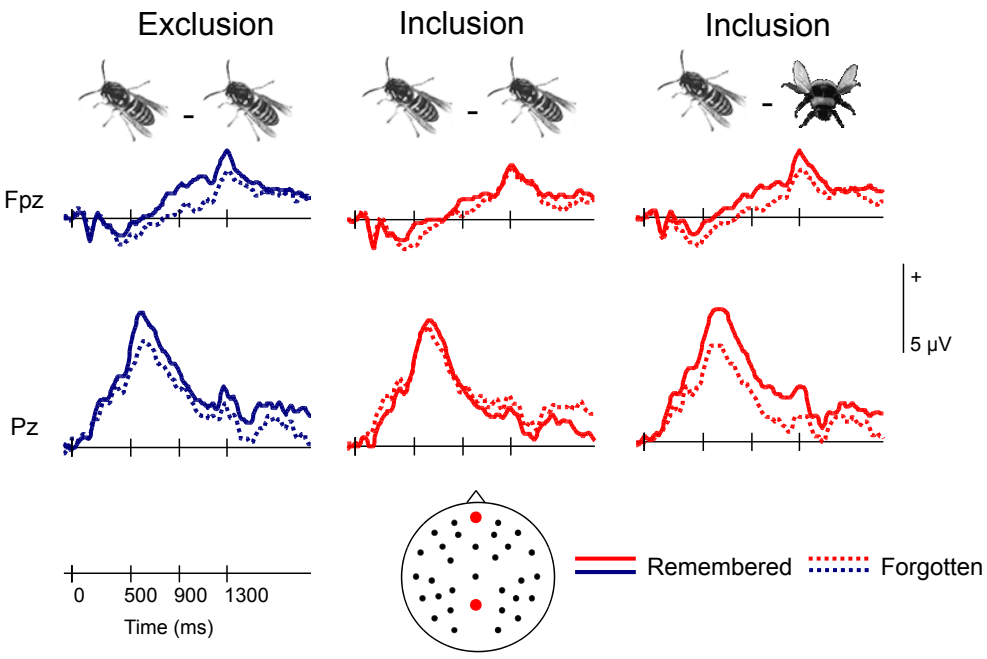

Figure 12. Encoding-related neural activity. Group averaged ERP waveforms at study are compared for later remembered (solid line) versus forgotten (dotted line) photographs later probed with copy cues in the exclusion task (highlighted in blue); with copy cues (middle) and with exemplars (right) in the inclusion task. The waveforms for two representative midline electrode sites (equivalent to Fpz and Pz of the international 10/10 system) are displayed. Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes.

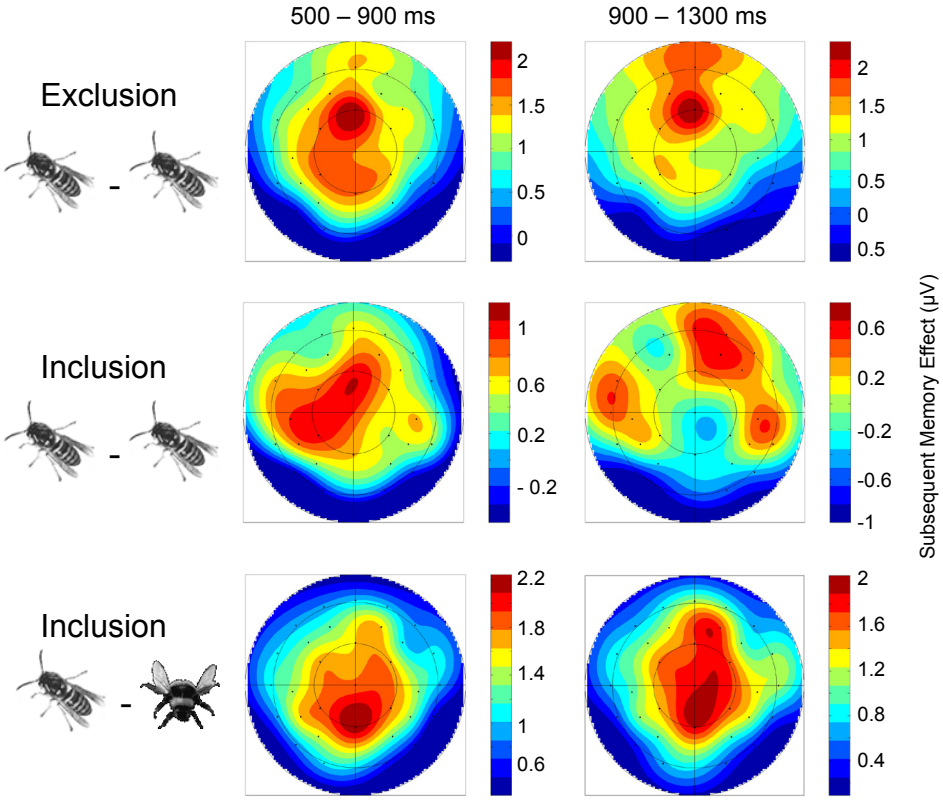

Figure 13. The spline maps illustrate the scalp distribution of the difference activity between subsequently remembered and forgotten photographs cued with copy cues in the exclusion task (top); with copy cues in the inclusion task (middle) and probed with an exemplar in the inclusion task (bottom) in the latency region of 500-900 ms and 900-1300 ms.

2.3.4 DISCUSSION

Experiment 3 addressed the question whether encoding-related activity varies depending on whether memory was tested with exclusion (specific focus) or inclusion (general focus) memory tasks (Jacoby et al., 1993). More specifically, it was assumed that the exclusion task emphasised perceptual retrieval processes and the inclusion condition conceptual attributes (Ecker & Zimmer, 2009; Ranganath et al., 2000). Experiment 3 aimed to elucidate whether perceptual and conceptual retrieval processes are associated with distinct encoding-related brain activity.

Overall memory performance was highest in the 'Concept' task for copy cues, followed by copy cues in the 'Picture' task. Exemplars in the 'Concept' task led to lower memory performance than in the other two conditions. 'Br's showed a similar pattern; participants were most liberal in accepting the test probes as old when the same pictures were shown in the concept task. Consistent with the previous literature (e.g. Park & Rugg, 2008), behavioural performance provided support for transfer-appropriate processing principle, because copy cues in the 'Concept task' led to a higher memory performance than exemplars in the 'Concept' condition. In line with the transfer-appropriate framework, correct old judgments were given quicker in the match condition than in the mismatch condition of the concept task. Crucially, the physical match did not per se determine memory performance, because copy cues in the 'Concept' condition lead to significantly higher memory accuracy and lower RT for remember responses than copy cues in the 'Picture' condition.

Qualitatively different encoding-related ERP effects as a function of the type of retrieval focus were expected based on the previous literature and the results in Experiments 1 and 2. While a more frontally distributed effect was predicted for items later cued in the 'Concept' condition, an effect pronounced over posterior locations was expected for pictures later probed in the picture task. The findings were only partly in line with the predictions. Encoding-related ERPs did not differ qualitatively depending on the type of retrieval focus. However, amplitude differences were evident in a later latency region between 900 and 1300 ms. Copy cues in the 'Concept' condition were not associated with a statistically reliable subsequent memory effect. In contrast, copy cues in the 'Picture' condition and exemplars in the 'Concept' condition elicited a widespread subsequent memory effect. In the two latter conditions, similar cognitive processes may have been engaged (Otten & Rugg, 2004).

These findings suggest that the mere retrieval focus (perceptual vs. conceptual) was not associated with distinct subsequent memory effects. Thus, encoding-related activity may not differ as a function of conceptual and perceptual retrieval focuses. However, this interpretation is inconsistent with previous findings showing that encoding-related activity varied with the type of retrieval cue and retrieval requirements (Bridger & Wilding, 2010; Otten & Rugg, 2007; Park & Rugg, 2008). Alternatively, the statistical power may have been too low to establish statistically reliable scalp distribution differences across conditions.

Intriguingly, the findings in the 'Concept' condition probed with copy cues did not resemble the subsequent memory effect shown in Experiment 1 and 2 for photographs in the match conditions. Studied photographs later cued in the same format elicited consistently a sustained subsequent memory effect over frontal electrode sites. Particularly, for copy cues in the 'Concept' condition the power may be little, because this condition had considerably less trials for the forgotten items in comparison to the other conditions. An alternative explanation for the absence of an effect for copy cues in the 'Concept' condition might be related to the possibility that these pictures were processed more variably with the emphasis on different types of attributes. In contrast, in the 'Picture' task participants needed to recollect specific pictorial features and in turn, had to engage consistently to some extent similar processes to confidently remember the picture. However, the more variable focus in the 'Concept' condition cannot explain solely these differences, because exemplars in the same retrieval task showed similar effects as the copy cues in the 'Picture' task. In the 'Concept' condition when cued with exemplars participants also may have had to remember specific details such as perceptual details from the studied image to decide that the specific category was studied before. Experiment 2 showed similar widely distributed subsequent memory effects for outlines and photographs that were later cued with the alternative probe. Together, these findings suggest that a physical mismatch may be associated with perceptual analysis processes. However, because widespread subsequent memory effects occurred in both 'Concept' task (for exemplar cues) and 'Picture' task (copy cues), this effect may reflect both conceptual and perceptual processes.

In the current experiment it may have been possible that the retrieval judgements in the 'Concept' and 'Picture' task relied on different types of recognition memory (Yonelinas, 2002). For instance, the absence of a subsequent memory effect in the 'Concept' condition might reflect a greater contribution of familiarity in comparison to the recognition judgements in the 'Picture' task (e.g. Voss & Paller, 2009). In the 'Picture' condition, participants most likely relied to some extent on recollection of specific details such as pictorial attributes to ensure that they had seen the exact item before. In contrast, in the 'Concept' condition a general feeling of knowing the object from the encoding task could have been sufficient to accept an item as old. In line with this interpretation, previous research investigating encoding-related activity showed evidence that subsequent memory effects associated with recognition judgements based on familiarity were smaller than effects related to recollection judgements (Paller & Wagner, 2002). Because Experiment 3 did not differentiate between R/K judgements, it is difficult to disentangle the contribution of familiarity and recollection related processes across retrieval conditions. However, statistical analyses of the retrieval–related ERPs (Appendix 2) did not reveal differences in midfrontal ERP effects that are usually associated with familiarity related processes. Moreover, a left-parietal effect (for review see Johnson & Friedman, 2000) was evident for all three conditions, suggesting no different contribution of the different kinds of recognition memories across retrieval tasks.

Another explanation for the absence of distinct subsequent memory effects as a function of retrieval focus effect may refer to the trial-by-trial engagement of specific retrieval orientations. Recent behavioural findings (Koutstaal, 2006) and a recent ERP study (Ecker & Zimmer, 2009) showed evidence that different retrieval strategies could be flexibly established on a trial-by trial basis. However, previous ERP studies reported also a significant advantage in maintaining different retrieval orientations when these were established in separate blocks (e.g. Johnson & Rugg, 2006). In contrast to a recent ERP study using a similar trial-by-trial manipulation (Ecker & Zimmer, 2009), the analysis of the retrieval orientation data in the current experiment did not reveal any significant differences as a function of the retrieval focus (see Appendix 2). Therefore, it may be likely that 'Concept' and 'Picture' tasks did not emphasize different retrieval processes as predicted. Instead maybe conceptual and perceptual attributes may have been emphasized in both tasks. The manipulation of retrieval orientations across subjects or across blocks, rather than within, might

optimise the separation of conceptual and perceptual processes. Moreover, the use of source memory tasks that emphasise the recollection of either conceptual details or perceptual details from the studied episode might help to disentangle the impact of perceptual and conceptual processes on the encoding-related brain activity. Finally, the use of stimulus material with minimal conceptual content (e.g. kaleidoscope images Voss & Paller, 2009) may help discern the functional role of different types of encoding-related brain activity

Experiment 3 demonstrated that a widespread subsequent memory effect may reflect conceptual and perceptual processes. The statistical power may have been too low to detect distinct processes as a function of the type of retrieval process. Experiment 3 showed further evidence that study-test congruency plays a role for the neural correlates of encoding.

Overall, the three ERP experiments suggest a direct role of the functional overlap of encoding and retrieval processes on the neural bases of long-term memory encoding, because encoding-retrieval overlap effects were evident briefly after item onset. However, because study-test congruency was evident only for pictorial information irrespective of the amount of perceptual information encoding-retrieval overlap may not be a universal organisational principle of the neural correlates of long-term memory encoding. Future studies need to elucidate whether the dissociation between frontally and posteriorly distributed subsequent memory effects is evident when using perceptual and conceptual manipulations at encoding and retrieval.

CHAPTER 3: THE IMPACT OF STUDY-TEST CONGRUENCY AND AMOUNT OF PERCEPTUAL INFORMATION ON THE NEURAL CORRELATES OF RETRIEVAL

3.1.1 EXPERIMENT 2: DOES RETRIEVAL-RELATED BRAIN ACTIVITY VARY WITH THE PERCEPTUALLY RICHNESS OF IMAGES ACROSS ENCODING AND RETRIEVAL?

Chapter 2 provided evidence that study-test congruency plays an important role for the neural correlates of memory formation. This effect was specific to pictorial information. In addition to investigating the neural correlates of memory encoding, Experiment 2 was designed to examine whether retrieval-related ERPs vary depending on the amount of perceptual information at encoding and retrieval. This is a relevant research question in the light of recent findings reporting material-specific and content-dependent retrieval-related brain activity (e.g. Galli & Otten, 2010; Johnson & Rugg, 2007; Khader, Heil & Rösler, 2005; Yick & Wilding, 2008).

Material-specific modulations of retrieval-related brain activity are in line with the transfer-appropriate processing framework (see also source memory framework; Mitchell & Johnson, 2009). Memory representations for an event are formed based on the encoding of its specific attributes such as conceptual or perceptual attributes. In turn, retrieval processes vary as a function of the retrieved content. Thus, the recollection of photographs of objects or faces may be associated with different brain regions at retrieval than words, because images for instance consist of more perceptual attributes than words.

In the same vein, neural models of episodic memory predict material-specific retrieval processes. The models state that successful memory retrieval depends on the reinstatement of the activity that was engaged when the item was initially encountered (e.g. Norman & O'Reilly, 2003, Rolls, 2000). In accordance with these neural models neuroimaging studies using fMRI reported that different brain regions were involved at retrieval depending on the type of stimulus material and processes engaged at encoding (Johnson & Rugg, 2007; Khader et al., 2005; Kahn et al., 2004; Wheeler et al., 2000; Woodruff et al., 2005;Wheeler et al., 2006).

However, due to the low temporal resolution of hemodynamic signals it is not clear whether material specific retrieval activity reflects indeed differences in processes related to the recovery of episodic information or whether these material-specific processes occur downstream of recollection such as retrieval monitoring or evaluation processes (cf. Johnson et al., 2008; Yick & Wilding, 2008). To dissociate better between these different kinds of retrieval processes and to understand the temporal nature of the material-specific retrieval effects, an acquisition technique is necessary that has a high temporal resolution, such as EEG (Rugg & Coles, 1995). Previous ERP retrieval studies investigated predominantly words as stimulus material. However, a handful of recent ERP studies compared directly the brain activity associated with the retrieval of different kinds of stimulus materials.

While words elicited recollection-related ERP effects that were pronounced over left parietal scalp locations (Johnson & Friedman, 2000), for both faces and photographs of objects a more widely distributed effect that was also pronounced over anterior scalp sites was reported (*faces:* Curran & Hancock, 2007; MacKenzie & Donaldson, 2007; Yovel & Paller, 2004; *photographs of objects*: Duarte et al., 2004; Johansson, Stenberg, Lindgren & Rosen, 2002; Kuo & Van Petten, 2006, Ranganath & Paller, 2000). Direct comparisons between words and faces and photographs within the same experiment demonstrated consistently more anteriorly distributed old/new effects for both faces and photographs, suggesting material-specific modulations of the neural correlates of recollection (Ally & Budson, 2007; Duarte et al., 2004; Galli & Otten, 2010; MacKenzie & Donaldson, 2009; Schloerscheidt & Rugg, 1997;Yick & Wilding, 2008). Although there is some initial evidence for material-specific recollection effects, little is known about the functional significance and interpretation of these material-dependent modulations.

Interestingly, contrary to the reviewed findings, an ERP study using simple line drawings (Curran & Clearly, 2003) instead of perceptually rich photographs of objects (Duarte et al., 2004; Schloerscheidt & Rugg, 1997) reported only a left-parietal effect such as observed for words. Since both photographs of faces and objects contain rich perceptual information in comparison to less complex line drawings (Curran & Clearly, 2003) and words (Wilding & Rugg, 1996), one could assume that the perceptually richness or the amount of perceptual information might be associated with the occurrence of retrieval-related effects over more anterior locations. If this

holds to be true, the material- specific modulation of recollection-related brain activity might be related to the amount of perceptual information rather than reflecting a pure distinction between pictorial and verbal information (Galli & Otten, 2010).

Crucially, a more frontally distributed effect for photographs and faces has been directly associated with reinstatement processes leading to the recovery of studied content (Galli & Otten, 2010; Johnson et al., 2008;Yick & Wilding, 2008) because these frontal modulations occurred before or at least within the same latency region when recollection-related ERP effects such as the left-parietal old/new effect are usually elicited (Johnson et al., 2008; Yick & Wilding, 2008). For instance, the recollection of pictures and faces may be associated with the recovery of more perceptual information from the studied episode than words.

However, to my knowledge there is no previous study that directly manipulated the stimulus material at study and test to disentangle whether the content at study or the qualities of the test probe affect the retrieval-related ERPs. Previous studies presented the same content or stimulus material respectively at encoding and retrieval, which makes it difficult to disentangle whether the retrieval-related brain activity varies purely with the encoded content (Johnson et al., 2008; Norman & O'Reilly, 2003; Rolls, 2000) or whether retrieval processes differ as a function of the stimulus type of the retrieval cue aiding the recovery of episodic information (Johnson, Kounios & Nolde, 1997; Leynes, Bink, Marsh, Allen & May, 2003). Therefore, the present study aimed to elucidate whether the retrieval-related ERP effect varies with the amount of pictorial information at encoding or rather differs depending on the amount of perceptual information of the test probe. This research question was directly addressed by manipulating the study-test congruency of outlines and photographs.

Perceptually impoverished outlines and gray scaled photographs of objects and animals were incidentally encoded in a size judgement task. After a delay, half of the encountered outlines and perceptually rich photographs were cued with the same format (photograph-photograph; outline-outline) and half were tested with the alternative stimulus material (photograph-outline; outline- photograph). A R/K recognition test was used. However, the analysis in this Chapter has been focused on remember responses, because the question of interest was focused on how

recollection-related ERPs differ depending on the amount of perceptual information. Based on the previous literature using stimulus material with perceptually rich information (*faces*: MacKenzie & Donaldson, 2009; Yick & Wilding, 2008; *photographs of objects*: e.g. Ally & Budson, 2007; Duarte et al., 2004) and item types containing less perceptual information (*words*: Galli & Otten, 2010; Schloerscheidt & Rugg, 1987; *line drawings*: Curran & Clearly, 2003) it was expected that perceptually impoverished outlines would be associated with an old/new effect pronounced over left-parietal locations. In contrast, photographs were expected to elicit an old/new effect with a more widespread distribution and with the contribution of anterior locations.

Material-specific retrieval processes may reflect the reinstatement of qualitatively different encoding processes (e.g. Norman & O'Reilly, 2003) or recollected memory representations (Elward & Wilding, 2010; Vilberg et al., 2006). In this case, one would expect different ERP effects depending on the amount of perceptual information at encoding irrespective of the amount of perceptual information at test. Alternatively, the material-specific old/new effects might be influenced by the amount of pictorial information at test according to studies showing evidence that the left-parietal effect is affected by the type of test format.

3.1.2 METHODS

The stimulus material, experimental procedure and EEG acquisition are the same as outlined in Chapter 2. The method section highlights only the differences to the methods in Chapter 2.

PARTICIPANTS

Twenty-four native English speakers were included in the retrieval analysis (n = 24, 13 women, mean of age 21 years, range 18-27 years). For more detailed information see Experiment 2 in Chapter 2.

EEG DATA ANALYSIS

The filtering, re-referencing and down sampling procedure resembles the one used in experiment 2 of Chapter 2. Epochs of 2048 ms duration surrounding photograph and outline onsets were extracted from the retrieval data. Epochs started 100 ms before item onset. ERP waveforms were created for each subject and electrode site for outlines and photographs by averaging epochs related to remember and correct new judgments in the recognition memory test. The artifact correction for blinks, drifts, eye movements, amplifier saturation and muscle tensions has been already described in experiment 2 of Chapter 2. In each condition, ERPs were based on a minimum of 14 artifact-free trials. The mean number of trials (range in brackets) for remember responses for the outline-outline, photograph-outline, photograph-photograph and outline-photograph conditions were 36 (20-58), 28 (15-56), 39 (16-63) and 28 (14-59). The mean number of trials for correct rejections for new outlines and new photographs were 60 (38-81) and 61 (38-80).

To investigate how the amount of perceptual information at study and test affects retrieval success-related brain activity, old-new effects (see for review Johnson & Friedman, 1992) were compared across the congruent and incongruent conditions and outline and photograph conditions. These analyses focused on activity elicited by photographs and outlines that were given remember versus correct new judgments in the recognition test, because the research question was focused on how recollection-related brain activity varies as a function of the amount of pictorial information.

Initial repeated measures ANOVAs included the within-subject factors study-test congruency (match/mismatch), amount of pictorial information (outline/photograph), old/new and site (32 electrodes, see Figure 3 for montage). In case of significant interactions between old/new and site subsidiary analyses were conducted to understand the nature of the interaction. These analyses incorporated only a subset of electrodes that were partitioned in location (anterior/posterior), hemisphere (left/right) and electrode (48, 43, 33, 38, 22, 21, 46, 30, 16, 40, 25, 12) within-subject factors. A partition in left anterior, right anterior, left posterior and right posterior electrode clusters is a well established analysis procedure in the previous retrieval literature to investigate recollection-related ERP effects (e.g. Galli & Otten, 2010). Only effects involving old/new are reported.

For factors with more than two levels, Greenhouse-Geisser corrected *p* values and degrees of freedom are reported to control for nonsphericity (Keselman & Rogan, 1980). Scalp distribution differences across conditions were established after scaling the data with the max/min method to remove overall amplitude differences (McCarthy & Wood, 1985). For a detailed description see Chapter 2.

3.1.3 RESULTS

BEHAVIORAL DATA

ENCODING TASK

The RT results across the 24 participants resembled the pattern of results in Experiment 2 of Chapter 2 for a subset of 19 participants. Size judgments on outlines took on average 765 ms (SD = 120 ms) and 763 ms (SD = 114 ms) in the match condition and in the mismatch condition, respectively. For photographs, RTs were 728 ms (SD = 111 ms) and 737 ms (SD = 105 ms). An ANOVA comparing mean response times across study-test congruency and amount of pictorial information revealed a significant main effect of amount of pictorial information (F (1, 23) = 44.57; $P < .001$), indicating a longer RT for outlines (M = 764 ms; SD = 24 ms) than photographs (M = 732 ms; SD = 22 ms) during the study phase.

MEMORY TEST

Recognition performance and RT according to the amount of perceptual information in the congruent and incongruent condition across the 24 participants are shown in Tables 13, 14 and 15.

The ANOVA across both recollection- and familiarity-based memory performance revealed overall a main effect of study-test congruency ($F(1, 23) = 67.96$; $p < .001$) and an interaction between study-test congruency and amount of pictorial information ($F(1,23) = 10.93$; $p = .003$). Subsidiary analyses indicated a study-test congruency effect for both outlines ($t(23) = 5.43$, $p < .0001$) and photographs ($t(23) =$

7.69, $p < .0001$). Moreover, photographs as test probes were associated with a higher overall memory accuracy than outlines, but only in the congruent condition ($t(23) = 2.14$, $p = .044$), other P = .06.

Although the ANOVA did not reveal a significant difference depending on the recognition type, memory accuracy based on recollection is reported separately, because the ERP analysis incorporated only remember responses. For outlines, the proportion of recollected items was 0.40 and 0.31 in the match and mismatch condition, respectively. For photographs, these values were 0.45 and 0.29. Outlines and photographs were both better recollected when probed in the same than in the alternative format (see Table). Similar pattern of results were evident as for the analysis across both recognition types. The ANOVA on the recollection data resulted in a significant main effect of study-test congruency ($F(1,23) = 102.51$; $p < .001$). Items that were later probed in the same presentation mode were better recollected than items in the alternative mode. Moreover, the analysis gave rise to a significant interaction between study-test congruency and amount of pictorial information ($F(1,23) = 5.47$, $p = .002$). Follow up paired t-tests resulted in significantly greater recollection performance for items cued with congruent probes than with incongruent cues for both outlines ($t(1, 23) = 5.02$; $p < .001$) and photographs ($t(1, 23) = 7.62$; $p < .001$). Recollection based memory performance did not differ between photographs and outlines within the congruent ($p = .059$) and incongruent condition ($p = .27$). Remember responses were more quickly given when items were cued in the same mode of presentation at test ($F(1, 23) = 17.28$, $p < .001$) for outlines and photographs, other $p < .10$). Correct responses to new photographs (M =1013 ms; SD = 246 ms) were given quicker than to new outlines (M = 1046 ms; SD = 253 ms): $F(1, 23) = 2.15$; $p = .040$).

Table 13. Recollection and familiarity estimates for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N = 24).

Study type	Test type	Recollection	Familiarity
Photograph	Photograph	0.45 (0.15)	0.27 (0.18)
	Outline	0.29 (0.13)	0.15 (0.13)
Outline	Outline	0.40 (0.12)	0.25 (0.15)
	Photograph	0.31 (0.14)	0.19 (0.12)

Values are across-subject means (SD).

Table 14. Mean proportion of remember, know, new responses for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N=24).

Study type	Test type	Remember	Know	New
Photograph	Photograph	0.51 (0.16)	0.20 (0.11)	0.29 (0.14)
	Outline	0.35 (0.15)	0.20 (0.11)	0.45 (0.17)
Outline	Outline	0.46 (0.14)	0.23 (0.12)	0.31(0.11)
	Photograph	0.38 (0.15)	0.19 (0.12)	0.43 (0.13)
New	Photograph	0.06 (0.04)	0.12 (0.07)	0.82 (0.09)
	Outline	0.06 (0.05)	0.13 (0.08)	0.81 (0.09)

Values are across-subject means (SD).

Table 15. Mean RT of remember, know, new responses for photographs and outlines that were cued in the congruent and incongruent mode of presentation (N=24).

Study type	Test type	Remember	Know	New
Photograph	Photograph	941 (157)	1158 (504)	1046 (275)
	Outline	994 (175)	1144 (470)	1056 (257)
Outline	Outline	961 (157)	1147 (401)	1066 (268)
	Photograph	973 (178)	1255 (396)	1034 (250)
New	Photograph	1012 (197)	1245 (348)	1013 (246)
	Outline	919 (446)	1176 (427)	1046 (253)

Values are across-subject means (SD).

EVENT-RELATED POTENTIALS

Figure 14 shows the grand averaged ERP waveforms for outlines and photographs test items that were studied in the congruent and incongruent presentation mode. ERPs elicited by correct remember judgements are compared with ERPs elicited by correct new judgements across outlines and photographs in the congruent and incongruent condition. Between approximately 300 and 500 ms after item onset, both outlines and photographs in the congruent condition elicited a positive-going modulation for remembered relative to correct new responses with a maximum over frontocentral electrode sites. In contrast for outlines and photographs in the incongruent condition, a positive-going modulation was less pronounced frontally and more widely distributed (see Figure 15 and Figure 16 and Figure 17 for scalp distribution map).

After around 500 ms outlines that were associated with correct remembered responses were associated with left posterior distributed positive-going modulations, regardless of whether the studied item was an outline or a photograph. In comparison to outlines, photographs elicited a widely distributed old/new effect that was pronounced over right anterior electrode sites, again regardless of the studied image type.

These observations were confirmed by the statistical analyses. Old-new effects were quantified by measuring mean amplitude values in the latency regions from 300-500 ms, 600-900 ms and 900-1200ms. Those time windows were chosen based on visual inspection of the waveforms and are consistent with previous ERP retrieval studies (Curran, 2000; Schloerscheidt & Rugg, 1997; Schloerscheidt & Rugg, 2004). Although a priori predictions were only focused on the middle time region, an earlier and later latency region were also analysed to test whether the effect of the amount of perceptual information is recollection-specific and unrelated to familiarity-related processes (Curran, 2000; Woodruff et al., 2006) or post-retrieval processes (Cruse & Wilding, 2009; Hayama & Rugg, 2009).

300-500 MS

Within the first latency region (300-500 ms) the initial analysis revealed a significant interaction between study-test congruency, old/new and site ($F(3.9,88.9) = 4.20$, $p = .004$). Subsidiary analyses with the within subject factors location (anterior/posterior), hemisphere (left/right) and site (48, 43, 33, 38, 22, 21, 46, 30, 16, 40, 25, 12) revealed a significant interaction between study-test congruency, old-new and location ($F(1,23) = 9.54$, $p = .005$). Separate analysis for congruent and incongruent cues, revealed only a significant interaction between old/new and location for the congruent cues ($F(1,23) = 11.17$, $p = .003$; other $p = .461$). These findings indicate a midfrontal old/new effect only for test items that were congruent to the studied presentation mode (anterior: 1.76 μV vs. posterior: 0.98 μV) regardless of the amount of pictorial information.

600-900 MS

In the second latency region, the initial ANOVA revealed a significant interaction between amount of perceptual information, old/new and site ($F(3.2,73.3) = 3.31$, $p = .022$). Subsidiary analysis on the partition of electrodes resulted in a significant interaction between amount of pictorial information, old-new, location ($F(1,23) = 7.04$, $p = .014$) and hemisphere ($F(1,23) = 4.65$, $p = .042$).

Separate analyses on anterior and posterior scalp locations resulted only in a significant difference between amount of pictorial information and old/new over posterior electrode locations ($F(1,23) = 13.25$, $p = .001$; anterior sites $p = .585$), indicating a significant stronger old/new effect for outlines (4.30 μV) in comparison to photographs (3.09 μV) over parietal sites. Moreover, the analyses on posterior locations revealed a significant interaction between amount of pictorial information, old/new and hemisphere ($F(1,23) = 6.83$, $p = .016$).

Separate analyses for outlines ($F(1,23) = 6.64$, $p = .017$) and photographs ($F(1,23) = 7.27$, $p = .013$) gave both rise to a significant interaction between old/new, location and hemisphere. Only for outlines a significant interaction between location and old/new was found ($F(1,23) = 5.08$, $p = .034$), suggesting an overall stronger old/new effect over parietal (4.30 μV) than frontal sites (3.55 μV). Moreover, for outlines, the interaction between old/new and location was only significant over the left hemisphere ($F(1,23) = 5.43$, $p = .029$, over right hemisphere $p > .890$), suggesting a maximum over left parietal sites.

In contrast, for photographs, the interaction between old/new and location was only significant over the right hemisphere ($F(1,23) = 9.61$, $p = .005$, other $p > .941$), indicating a right frontally distributed old-new effect. The interactions between the amount of pictorial information and 32 sites remained significant after scaling the data ($F(3.2, 72.8) = 9.59$; $p = .03$) (McCarthy & Wood, 1985). Moreover, the interaction between the amount of pictorial information and anterior/posterior location ($F(1,23) = 6.94$, p = .015) and hemisphere ($F(1,23) = 5.54$, $p = .041$) remained significant after scaling across the cluster partitions. For both outlines and photographs, the interactions with location and hemisphere were also significant after scaling the data ($F(1,23) = 6.63$, $p = .017$; $F(1,23) = 8.43$, $p = .003$).

In sum, the findings in the second latency region indicate that outlines as test probes elicited an old/new effect with its maximum over left-parietal locations irrespective of the amount of pictorial information at study. In contrast, photographs at test were associated with a significant weaker old/new effect over parietal locations and were associated with a more widespread distribution that was pronounced over right anterior sites.

900-1200 MS

Within the third time region, the ANOVA across all 32 sites revealed a significant interaction between the amount of pictorial information and old/new ($F(1,23) = 8.91$, $p = .007$) and site ($F(4.3,98.1) = 4.32$, $p = .002$), indicating a stronger old/new effect for outlines (3.77 μV) than photographs (2.86 μV). Moreover, the analysis revealed a significant interaction between study-test congruency and old/new ($F(1,23) = 6.47$, $p = .018$), suggesting a stronger old/new effect for incongruent (3.67 μV) than congruent probes (2.96 μV). Furthermore, the analysis resulted in a significant interaction between study-test congruency, old/new and site ($F(5.7,131.9) = 3.89$, $p = .002$).

Subsidiary analyses on the partition of a subset of electrodes were conducted to understand the nature of the interactions. The ANOVA revealed a significant interaction between amount of pictorial information, old/new and location ($F(1,23) = 9.48$, $p = .005$) and between study-test congruency, location and old/new ($F(1,23) = 13.19$, $p = .001$).

Subsidiary analyses revealed only a significant interaction between amount of pictorial information and old/new over posterior sites ($F(1,23) = 22.99$, $p < .0001$; other $p = .185$). These findings indicate that outlines (3.97 μV) were associated with a bigger old/new effect than photographs (2.86 μV) over posterior electrode sites. Furthermore, only the analysis over posterior sites revealed a significant interaction between study-test congruency and subsequent memory ($F(1,23) = 19.98$, $p < .0001$), indicating a stronger old/new effect for incongruent probes (3.42 μV) than congruent cues (2.35 μV) over parietal sites.

The interaction between the amount of pictorial information and both 32 electrode sites ($F(4.3,98.9) = 4.14$, $p = .003$) and anterior/posterior locations ($F(1,23) = 5.59$, $p = .027$) remained significant after scaling the data. Similar pattern of results were obtained incorporating the factor study-test congruency before and after scaling the data (across 32 sites: $F(5.4,125.1) = 3.57$, $p = .004$; across electrode partition: $F(1,23) = 11.99$, $p = .002$).

ANALYSES ACROSS THE THREE TIME INTERVALS

The analyses across time intervals revealed a significant interaction between time interval, study-test congruency, old/new and location when comparing the 300-500 ms latency region with the 600-900 ms time region ($F(1,23) = 9.87$, $p = .005$). The comparison between the second and third time interval resulted also in a significant interaction between study-test congruency, old/new and location ($F(1,23) = 10.42$, $p = .004$), indicating that the middle latency region was associated with qualitatively different effects than the first and third time regions.

In summary, retrieval-related activity within the recollection-related latency region varied qualitatively depending on the amount of pictorial information of the test item irrespective of the study-test congruency of presentation mode. Outlines at test elicited an old-new effect pronounced over left posterior sites. In contrast, photographs were associated with a significant weaker old/new effect over parietal locations, but with a more widespread distribution that was pronounced over right anterior sites.

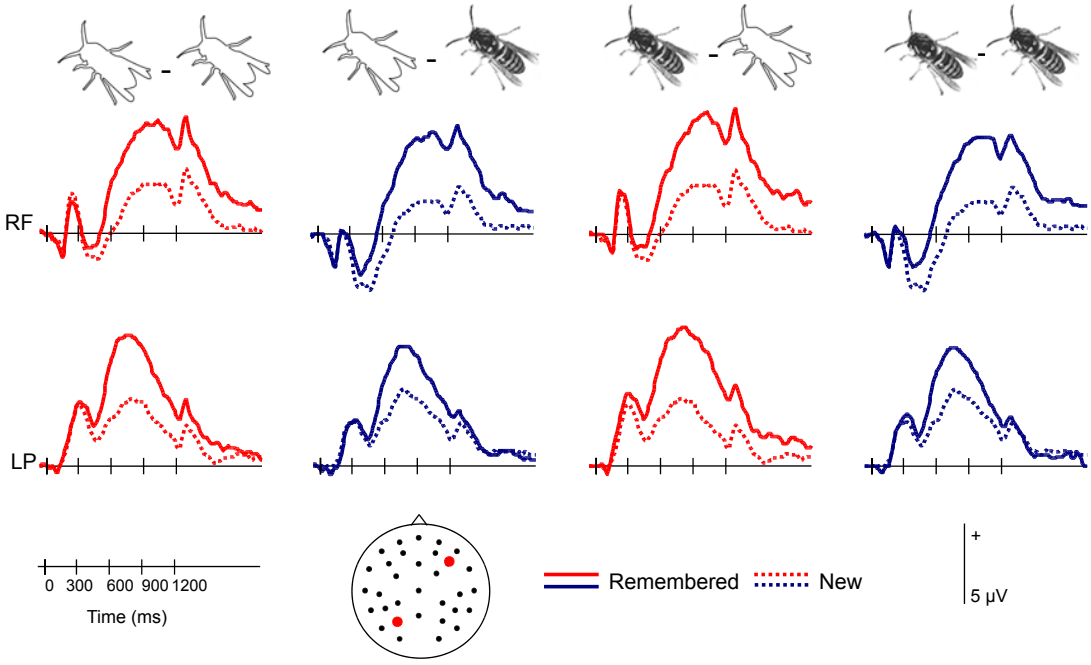

Figure 14. Retrieval-related neural activity. Group averaged ERP waveforms at test are compared for remembered (solid line) versus correct new responses (dotted line) for the outline-outline condition, outline-photograph condition, photograph-outline and photograph-photograph condition. The waveforms for two representative electrode sites (equivalent to LP and RF of the international 10/10 system) are displayed. Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes.

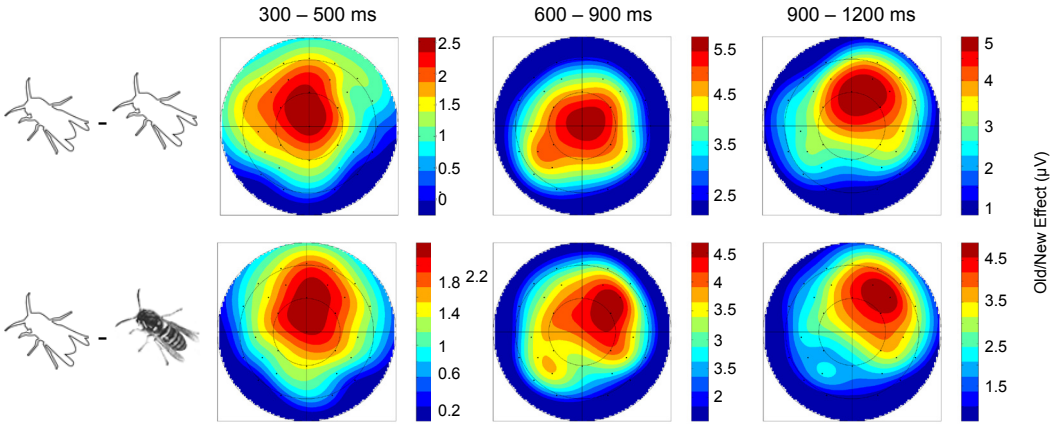

Figure 15. The spline maps illustrate the scalp distribution of the difference activity between remembered and correct new responses for the outline-outline condition and outline-photograph condition in the latency region of 300-500 ms, 600-900 ms and 900-1200 ms.

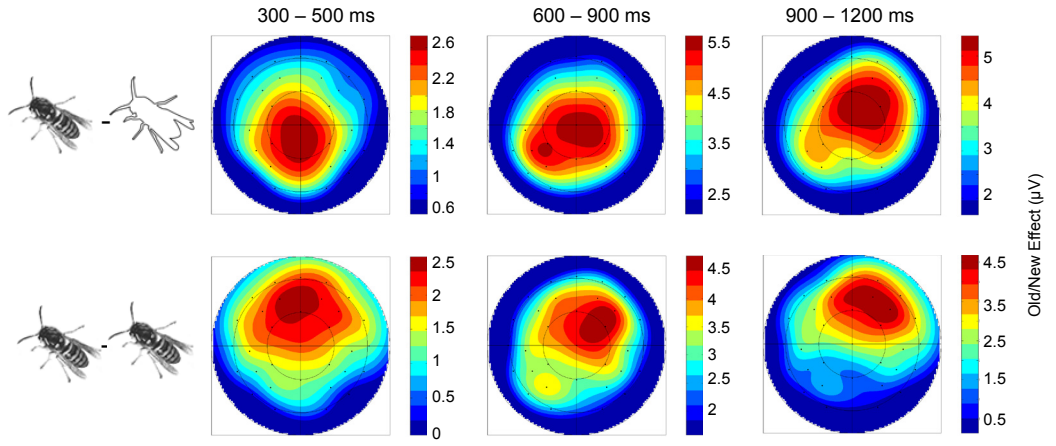

Figure 16. Scalp distributions of the ERP difference between remembered and new responses for the photograph-outline and photograph-photograph condition in the three latency regions.

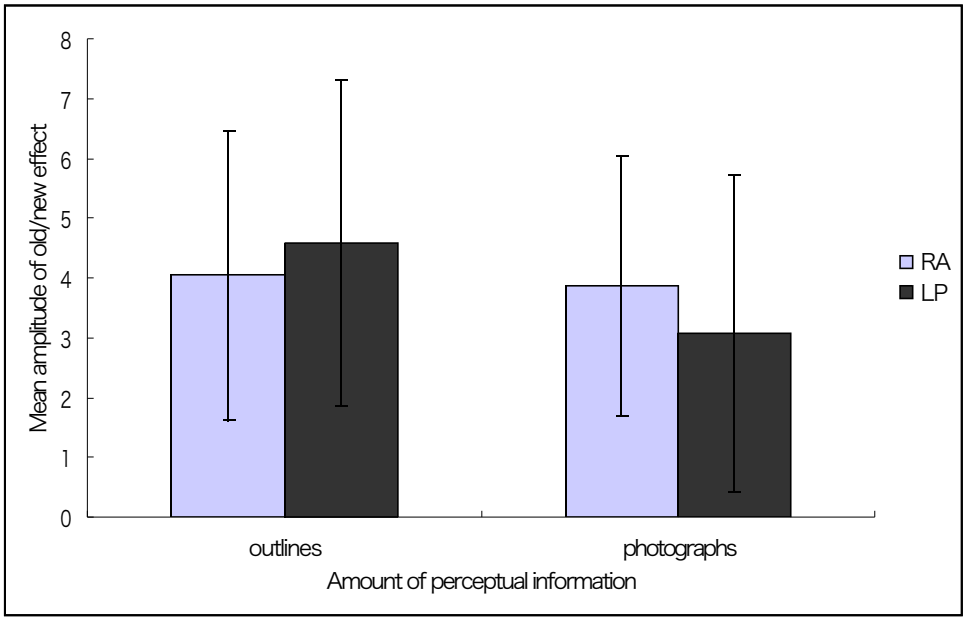

Figure 17. Mean amplitude of the old/new effect (remember minus correct new responses) in the latency region of 600-900 ms at a left-parietal electrode (LP; highlighted in dark grey) and a right frontal electrode (RF; highlighted in bright grey) for outlines as test probes (left) and photographs as test probes (right). Error bars indicate SD.

3.1.4 DISCUSSION

The present experiment addressed whether retrieval-related brain activity varies as a function of the amount of perceptual information at encoding and retrieval. This question was addressed by presenting intermixed perceptually impoverished outlines and grey scaled photographs at study. At test, half of the items were presented in the same presentation mode at study and half in the alternative presentation mode.

The behavioural findings resemble the findings reported in Experiment 2 in Chapter 2 and provide strong support for the study-test congruency effect. RT for remembered responses, overall memory performance and memory performance based on recollection showed an advantage for items later cued in the congruent presentation mode. Those findings are in line with Experiment 1 in Chapter 2 and previous studies suggesting that memory benefits from an overlap between encoding and retrieval processes (Jacoby, 1996; Mulligan & Osborn, 2009; Park & Rugg, 2008; Schloerscheidt & Rugg, 2004).

The ERP data in the early time region, between 300 and 500 ms, are consistent with the behavioural findings. Brain activity related to retrieval success differed qualitatively depending on the study-test congruency of presentation mode. Outlines and photographs that were congruent to the presentation mode at study elicited a midfrontal old/new effect between 300 and 500ms. In contrast, for incongruent cues the early old/new effect was widely distributed. These findings are consistent with previous ERP studies showing that an early frontal old/new effect is present or stronger when the presentation mode between study and test item is the same (Ecker et al., 2007; Schloerscheidt & Rugg, 2004).

In contrast, ERPs associated with retrieval success in the middle time region did not differ depending on the study-test congruency of presentation mode. Interestingly, the old-new ERP effects varied as expected with the amount of pictorial information. Crucially, the experimental design enabled investigating whether retrieval related activity was affected by the amount of pictorial information at study or test. The findings provide evidence that the amount of perceptual information at retrieval rather than the studied content affects the neural correlates of retrieval success.

Perceptually impoverished outlines at retrieval elicited a recollection-related ERP effect pronounced over left parietal electrode sites irrespective of the encoded amount of perceptual information. In contrast, grey scaled photographs were followed by a more widespread old/new effect that was predominantly distributed over the right hemisphere over anterior locations. These findings are in line with cognitive models of episodic memory that predict distinct recollection processes as a function of the item type (Mitchell & Johnson, 2009). Moreover, the topographical dissociation resembles previous ERP findings that showed qualitatively different effects for words in comparison to photographs and faces (Ally & Budson, 2007; Galli & Otten, 2010; MacKenzie & Donaldson, 2009; Yick & Wilding, 2008). While both photographs and faces were associated with widespread old/new effects that were predominantly distributed over anterior sites (Ally & Budson, 2007; Galli & Otten, 2010), words elicited a left-posterior effect that is usually associated with generic recollection processes (Wilding & Rugg, 1996). Moreover, the current findings for outlines resembled the left-parietal old/new effect that was reported for simple line drawings in a previous ERP study (Curran & Clearly, 2003).

This current experiment replicated and extended the previous research by demonstrating that the recollection-related ERP effects do not solely vary as a function of pictorial versus verbal materials (Galli & Otten, 2010; MacKenzie & Donaldson, 2009), but rather differ depending on the amount of perceptual information. In comparison to photographs of faces or objects, outlines of objects contain less perceptual information that may be related to different retrieval processes that underlie distinct brain regions. Although faces were not manipulated in the present experiment, the findings may be in line with recent suggestions that faces are not retrieved in a 'face-specific' manner, but might be similarly processed and retrieved as other perceptually rich images (cf. Galli & Otten, 2010). A future study could directly address whether pictorially richer images of faces and images of faces with less pictorial information such as outlines of faces elicit a similar dissociation between left-parietal and right anterior ERP effects as between photographs and outlines in the present experiment.

To what cognitive processes are the retrieval effects in the current experiment related? The more widespread and right anterior distribution of old/new effects for photographs in comparison to outlines might reflect processes related to the retrieval of perceptual details. Intriguingly, a direct comparison between scalp location and image type revealed only significant differences as a function of the amount of pictorial information over left parietal electrode sites. Outlines elicited a stronger left-parietal effect than photographs. The stronger contribution of left-parietal locations for outlines in comparison to photographs is consistent with previous studies showing larger left-parietal effects for words in comparison to photographs of faces and objects (Galli & Otten, 2010; MacKenzie & Donaldson, 2009). In line with MacKenzie and Donaldson (2009) comparing names and faces, outlines were followed by an old/new effect over left parietal sites and photographs elicited old/new effects bilaterally over posterior locations. MacKenzie and Donaldson (2009) reported additionally to a more pronounced left-parietal effect for words also a stronger contribution of anterior locations for faces in comparison to words. Another recent ERP study comparing words and faces reported only differences over anterior sites depending on the item type and similar contributions over left-parietal scalp sites for both stimulus materials (Yick & Wilding, 2008). In contrast, the current findings suggest that the topographical difference between retrieval-related ERP effects for outlines and photographs seem to be driven by differences over left-parietal locations.

Thus, alternatively to the interpretation of a relative stronger contribution of frontal locations for photographs, the functional significance of feature-specific retrieval effects could also be interpreted in terms of a relative smaller left-parietal contribution for photographs in comparison to outlines. Previous studies reported an increase in amplitude of the left-parietal old/new effects for items that were encountered in deep encoding tasks (Rugg et al., 1998; Wilding & Rugg, 1996), for items that were retrieved in source memory tasks (Donaldson & Rugg, 1999) and for a greater extent of retrieved information (e.g. recollection of 1 versus 2 sources; Vilberg & Rugg, 2008; Wilding, 2000).

At first glance, it seems to be counterintuitive to assume that perceptually impoverished outlines elicited a larger left-parietal effect, because outlines contained actually less pictorial information than photographs and should be associated with the retrieval of less information. However, a larger left-parietal old/new effect for outlines might be interpreted in the light of a previous ERP study that compared retrieval-related ERP effects for high frequency and low frequency words (Rugg et al., 1995). Rugg et al. (1995) reported a larger left-parietal effect for less frequent words in comparison to more frequency words. The authors suggested that the recollection of high frequency words was associated with less information in comparison to low frequent words. This interpretation was based on the fact that less familiar items may be incorporated in more distinct memory representations that in turn lead to the reinstatement of more encoded qualities.

In the same vein, one could suggest that outlines are less common or more novel respectively than perceptually richer photographs. Moreover, unfamiliar items such as outlines of objects may be more distinct than familiar photographs (Rugg et el, 1995) that in turn might have led to a greater left-parietal effect. However, the behavioural findings are inconsistent with this interpretation. Recollection (i.e. proportion of remembered minus proportion of false alarms) did not differ significantly between photographs and outlines and overall photographs tend to be remembered to a greater extent than outlines. Another observation that is inconsistent with the outlined interpretation is related to the fact that outlines as test probes were associated with larger left-parietal effects in comparison to photographs irrespective of the encoded content (i.e. whether it was encoded as outline or photograph). Therefore, it is rather implausible that the larger left-parietal effect for outlines reflects the recovery of more distinct encoded content.

The present findings challenge the interpretation based on neural models of episodic memory (Norman & O'Reilly, 2003) that claim that the differences in recollection-related brain activity reflect reactivation of different studied content or memory representations, respectively. Instead, the findings indicate that the modulation of the old/new effect as a function of the amount of the pictorial information at test might reflect processes that orient to the pictorial information of the retrieval cues. The current finding is partly consistent with a previous study comparing words and faces (MacKenzie & Donaldson, 2009). MacKenzie and Donaldson (2009) paired faces and names at encoding and presented either face cues or name cues at retrieval. When keeping the stimulus material at encoding identical, only face cues at test elicited a more anterior effect. MacKenzie and Donaldson (2009) interpreted the effect in terms of the reinstatement of different encoded contexts (name cue – face context; face cue – name context). Irrespective of the validity of this interpretation, those findings highlight that the effect may be at least partly affected by the stimulus material of the test probe or dependent on an interaction between study content and test probes, because solely recapitulation of encoded faces that were cued with names was not sufficient to elicit an anterior effect. Only when memory was later tested with face cues was an anterior effect shown.

Alternatively, the modulation of the old/new effect may reflect rather material-specific post-retrieval processes that are engaged after the studied episode has been recovered such as retrieval monitoring or evaluation processes (Cruse & Wilding, 2009, 2011; Hayama & Rugg, 2008). Previous studies reported larger late right-frontal ERP old/new effects between around 800 and 1400 ms in a source judgement task that required the retrieval of contextual details in comparison to simple old/new recognition tests (Johnson et al., 1997; Senkfor & Van Petten, 1998). Those findings led to the assumption that late right-frontal modulations may reflect retrieval monitoring processes. In the same vein, a right-frontal old/new effect was more pronounced in tasks that were associated with lower memory accuracy (Rugg, Allan & Birch, 2000). However, the behavioural findings of the present study are inconsistent with this interpretation. Memory performance based on recollection did not differ significantly between outlines and photographs. Furthermore, correct new judgements for photographs that were associated with more frontal contributions were associated with significantly quicker RTs than correct new judgements for outlines. Crucially, the early occurrence of the content-specific effect in the present study is not

consistent with this interpretation (see also Yick & Wilding, 2008). The comparisons across time intervals between the middle and latest latency regions (900-1200 ms) suggest also that both time regions were associated with qualitatively different old/new effects and therefore may not share similar cognitive processes. Therefore, an interpretation in terms of material-dependent retrieval monitoring processes is rather implausible. The early occurrence of content-specific processes may reflect recollection-related processes directly related to the recovery of episodic information (Yick & Wilding, 2008).

Irrespective of the validity of those interpretations, the present experiment demonstrated feature-dependent retrieval processes within the same stimulus-quality. The present findings suggest that a more anterior contribution of recollection-related ERP effects might reflect processes related to the retrieval of perceptual information. Moreover, the present study showed evidence that the amount of the pictorial information of the test probe rather than the encoded quality affects the retrieval-related brain activity.

As yet, it is not clear whether the modulation associated with the amount of perceptual information varies in graded manner and whether a more anteriorly distributed old/new effect for photographs of objects represents an additional effect that overlaps in time with the left-parietal effect (MacKenzie & Donaldson, 2009;Yick & Wilding, 2008;). Future research needs to shed more light on this. For instance, in future studies a gradation of the perceptual information of the test cue on a continuum (i.e. from outlines over more detailed line drawings to perceptually richer photographs) may help to disentangle those processes and to understand whether the recollection-related effects vary in graded manner depending on the amount of perceptual information.

3.2.1 EXPERIMENT 4: DOES RETRIEVAL-RELATED BRAIN ACTIVITY VARY WITH THE DEGREE OF PERCEPTUAL INFORMATION?

The previous experiment demonstrated that recollection-related brain activity varies with the perceptually richness of the test probes. While perceptually impoverished outlines were associated with larger left-parietal old/new effects, perceptually richer photographs elicited a widespread old-new effect with a maximum over anterior sites of the right hemisphere.

As yet, it is not clear whether recollection-related brain activity grades with the amount of perceptual details, because perceptually richness was only manipulated on two levels in the previous experiment. The images contained either more (grey scale photographs) or less perceptual information (outlines). The use of an additional image type that consists of an intermediate level of perceptual attributes such as detailed line drawings may elucidate whether retrieval-related activity indeed grades as a function of the amount of perceptual attributes.

Participants saw intermixed three different kinds of images: perceptually impoverished outlines of objects, more detailed line drawings and grey scaled photographs of objects. In an incidental encoding task participants had to make a size judgement. After a short delay, studied and unstudied outlines, line drawings and grey scaled photographs were presented in an R/K recognition test. The manipulation of the amount of pictorial information on a continuum was expected to elucidate whether differences as a function of the amount of perceptual details are associated with differences in retrieval-related ERPs over anterior or rather parietal locations. Thus far, it is not clear whether material-specific differences in retrieval-related activity are driven by differences in left-parietal or right-frontal contributions. For instance, in an old/new recognition test Yick and Wilding (2008) reported no differences over left-parietal locations for faces and words, but an additional anterior old/new effect specific for faces. The authors suggested that the stronger contribution over anterior sites for faces possibly co-occurred temporally with a material-independent left-parietal effect that was evident for faces and words (see also Curran & Hancock, 2007; Mac Kenzie & Donaldson, 2007, Yovel & Paller, 2004). In contrast, in an R/K recognition test Donaldson and MacKenzie (2009) reported differences in the amplitude of the old/new effects for face and word cues over left-parietal as well as

over right anterior sites. These latter findings may suggest rather a gradation from a left parietal to anterior old/new ERP effect as a function of material, rather than a temporal overlap of two distinct processes.

A more anteriorly distributed old/new effect may be dissociable and might occur additionally to the left-parietal effect as a function of the amount of pictorial information an item contains (Yick & Wilding, 2008). In this case, any perceptually complex images such as line drawings or photographs may be associated with more widespread and anterior old/new effects. Alternatively, the retrieval-related brain activity may grade from either a maximum over left parietal sites up to more right frontal sites depending on the amount of pictorial information.

3.2.2 METHODS

The EEG acquisition was the same as the one outlined in Experiment 1 of Chapter 2.

PARTICIPANTS

The analyses were based on the data of 19 participants (mean age: 22 years, age range: 19-30 years, 10 female). The data of three further participants were excluded from the data analysis due to uncorrectable electrooculogram (EOG) artefacts (n = 2) and insufficient number of trials due to poor memory performance (n = 1). Ethical requirements and the selection criteria were the same as in Experiment 1 in Chapter 2.

STIMULUS MATERIAL

Stimuli were drawn from a pool of 308 black-and-white photographs of every day objects and animals. The photographs were selected from the Hemera Photo Objects suite and represented a subset of those photographs presented in Experiment 2. Corresponding outlines and more detailed line drawings were created in the same dimensions as the photographs by using the Adobe Photoshop software.

Nine sets of 32 items were selected pseudo randomly from the pool with the restrictions that half of the images in each set represented items that could fit into a shoebox, in their real size. Those sets were rotated across participants so that each item was presented equally often as a photograph, outline and line drawing during the study phase and as an unstudied photograph, outline and unstudied line drawing during the test phase. The study list consisted of six sets a 32 items. In total, the study list contained 64 photographs, 64 outlines and 64 line drawings (192 critical items). At test all 192 studied items were presented intermixed with 32 unstudied photographs, 32 outlines and 32 line drawings that were drawn from the item sets. The test phase consisted in total of 288 critical items. Consistent with Experiment 2, all of the studied items were presented in their mirror-reversed orientation at test. The memory test consisted of fewer items that might have made the memory test easier overall. The orientation change may have made the memory test more difficult and forced the participants to rely on recollection and stronger memories.

The study list was split in three blocks each containing 64 items. The test lists were divided in five test blocks. The remaining items in the stimulus pool were used for practice lists.

EXPERIMENTAL PROCEDURE

Experiment 4 also consisted of an incidental encoding task and a surprise recognition memory test after 30 minutes delay (see Figure 18). Photographs, outlines and more detailed line drawings were presented randomly intermixed in central vision on a white background for 1 sec. Preceding cues that were written in red Helvetica font were presented for 1.4 sec. The preceding cue and following image were separated by a blank period of 100 ms. The cues indicated 1.5 sec before image onset in what image type the upcoming item would be shown ('P' for a photograph; 'O' for an outline, 'L' for a line drawing). Volunteers were asked to focus on the cue (i.e. 'P', 'L' or 'O') to prepare for the upcoming image type. A fixation cross (+) was presented on the screen in periods where no image or cue were shown. The time between the items offset and the cues onset varied randomly between 1.5 and 3 sec. By pressing one of two buttons they decided whether the presented object would fit in a shoebox – in its real size. They were instructed to respond as quickly and as accurately as possible with their left or right index fingers. The responding hand was randomised across the participants. A short practise list was given prior to the study phase. The study phase took approximately 20 minutes.

At test, all studied items were presented again, intermixed with unstudied items (one third photographs, outlines and line drawings). Again, red cues starting 1.5 sec before each test item indicated in which image type the following item appeared ('P' for a photograph; 'L' for a line drawing, 'O' for a outline). Again, the participants were instructed to focus on the cues in order to prepare for the image type of the upcoming item. The time between the items offset and the cues onset varied randomly between 2.5 and 4 seconds.

As in Experiment 2 memory was tested with an R/K recognition task and volunteers were asked to press one of three buttons (see Chapter 2 Experiment 2 for detailed information). Again, the mapping of the responding fingers (i.e. index finger, middle finger and ring finger of the right hand) and corresponding decisions (i.e. remember, know, new) was randomised across subjects. Both accuracy and speed were stressed. A practise block preceded the test phase to familiarise the volunteers with the recognition task. The test phase took approximately 50 minutes. All images and preceding cues were presented with visual angles of 1.6 x 1.6° and 0.3° x 0.3°, respectively.

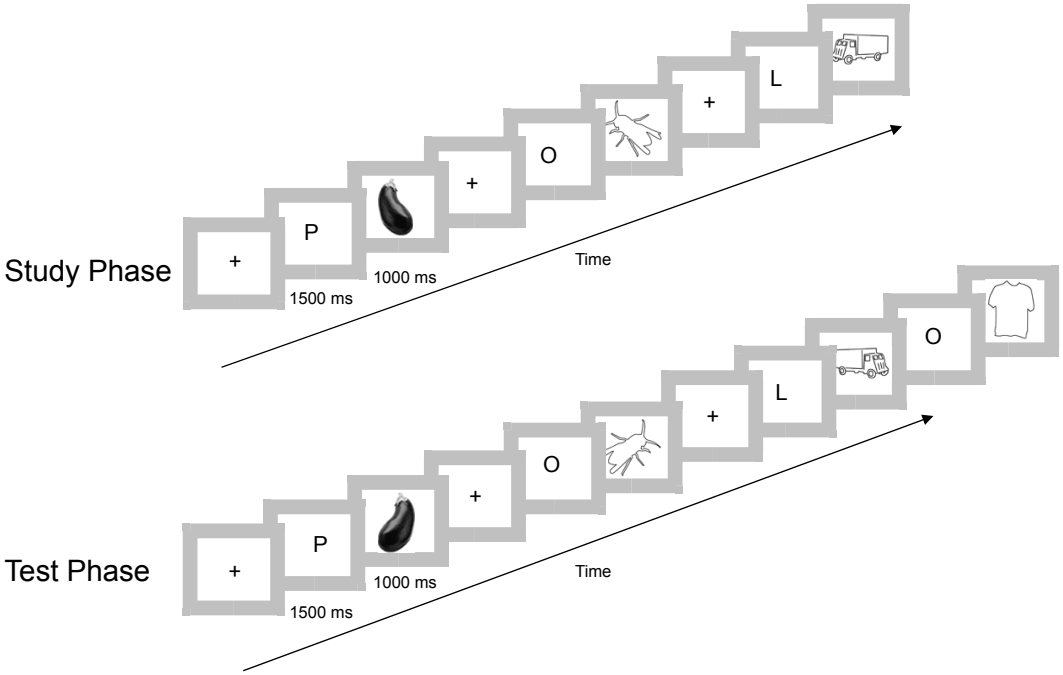

Figure 18. Experimental procedure. Participants saw a series of photographs, line drawings and outlines of objects and animals at study and test. Preceding letter cues indicated the item type of the upcoming image. At study, participants encoded the items incidentally within a size judgement task. In an R/K recognition test, participants saw intermixed studied and unstudied outlines, line drawings and photographs.

EEG DATA ANALYSIS

The information concerning the offline filter, sampling rate, re-referencing and epoching procedure was the same as described in the data analysis section in Chapter 1. ERP waveforms were created for each subject and each electrode by averaging epochs across photographs, line drawings and outlines separately for remember and correct new judgments in the recognition test. The same blink correction procedure and rejection criteria for horizontal eye movements, muscle artifacts and amplifier saturations were used as outlined in Experiment 1 in Chapter 2.

To investigate how the gradation of the amount of perceptual information affects recollection-related ERP effects, the analyses contrasted activity associated with remember and correct new responses across photographs, outlines and line drawings. ERPs corresponding to know responses were not considered, because only four participants had at least 14 artifact-free trials for items given know judgments. The mean number of trials (range in brackets) for remember responses for the photographs, outlines and line drawings were 30 (17-47), 25 (14-39) and 25 (14-39). The mean number of trials for correct rejections for new photographs, new outlines and new line drawings were 22 (14-31), 23 (14-31) and 23 (15-30).

Initially, a repeated measures ANOVA was conducted consisting of the within subject factors: gradation of perceptual information (photograph/line drawing/outline), old/new (remember/correct rejection) and sites (32 electrodes). Significant interactions involving old/new and sites were followed up with further analyses on a subset of electrodes cooperating the within-subject factors: location (anterior/posterior), hemisphere (left/right) and electrodes (48, 43, 33, 38, 22, 21, 46, 30, 16, 40, 25, and 12). Only effects involving old/new are reported. For factors with more than two levels, the reported *p* values and degrees of freedom were Greenhouse-Geisser corrected due to possible violations of the sphericity assumption (Keselman & Rogan, 1980). Significant interactions involving electrode sites were followed by analyses on scaled data to establish reliable scalp distribution differences (McCarthy & Wood, 1985; see Chapter 2 for detailed information).

3.2.3 RESULTS

BEHAVIOURAL DATA

STUDY DATA

The mean RTs for photographs, line drawings and outlines were 741 ms (SD = 98 ms) and 748 ms (SD = 86 ms) and 776 ms (SD = 113 ms) respectively. The ANOVA of RT with image type as within subject factor did reveal a significant difference (F(1.71, 30.73) = 7.35, p = .004). Further paired comparisons did result in significantly longer RTs for studied outlines in comparison to photographs (t(18) = -3.30, p = .004) and line drawings (t(18) = 2.66, p = .016). The RTs of photographs and line drawings did not differ significantly (p = .411). Accuracy was not considered due to the subjective nature of the encoding task.

TEST DATA

The proportions of hits and false alarms corresponding to remember and know responses and the estimations of recollection and familiarity separated according to the format in the match and mismatch group are shown in Table 16 and Table 17.

The ANOVA on the accuracy data with the memory type (recollection/ familiarity) and image type (photograph/outline/line drawing) resulted in a significant main effect of image type (F(1.73, 31.18) = 6.01; p = .008) and memory type (F(1,18) = 12.27, p = .003), other p = .118. Further paired comparisons suggest a higher overall memory performance for photographs in comparison to outlines (t(18) = 2.99, p = .008) and line drawings (t(18) = 2.83, p = .011). The overall memory performance for outlines and line drawings did not differ (p = .273).

A further ANOVA was conducted on memory performance based on recollection in isolation, because the ERP analyses were focussed on remember responses. This ANOVA showed the same pattern as the analysis on the overall memory performance (F(1.8, 31.7) = 14.31, p < .0001). The number of recollected photographs differed significantly from recollected outlines (t(18) = 4.32, p < .0001) and line drawings (t(18) = 4.45, p < .0001), other p = .281.

Response times for remember judgments did not show significant differences across the different image types, $p = .070$. Correct new responses did not differ depending on the image type ($p = .073$) (see Table 18).

Table 16. Recollection and familiarity estimates for photographs, line drawings and outlines (N = 19).

	Recollection	Familiarity
Photograph	0.55 (0.15)	0.33 (0.21)
Line drawing	0.46 (0.12)	0.33 (0.16)
Outline	0.44 (0.14)	0.31 (0.16)

Values are across-subject means (SD).

Table 17. Recognition memory performance for photographs, outlines and line drawings (N=19).

Image type		Remember	Know	New
Photograph	Old	0.58 (0.15)	0.17 (0.12)	0.25 (0.13)
	New	0.03 (0.04)	0.06 (0.06)	0.91 (0.06)
Line drawing	Old	0.49 (0.13)	0.21 (0.12)	0.30 (0.10)
	New	0.03 (0.03)	0.07 (0.07)	0.90 (0.08)
Outline	Old	0.47 (0.14)	0.22 (0.11)	0.31 (0.12)
	New	0.03 (0.05)	0.10 (0.06)	0.87 (0.07)

Values are across-subject means (SD).

Table 18. Mean RTs (ms) for photographs, outlines and line drawings (N=19).

Image type		Remember	Know	New
Photograph	Old	997 (195)	1196 (410)	1178 (300)
	New	611 (611)	1141 (808)	1020 (192)
Line drawing	Old	1010 (202)	1335 (257)	1180 (247)
	New	748 (743)	991 (640)	1044 (186)
Outline	Old	1030 (224)	1290 (228)	1197 (282)
	New	570 (662)	1141 (598)	1061 (212)

Values are across-subject means (SD).

EVENT-RELATED POTENTIALS

Figure 19 shows the group-averaged ERP waveforms for photographs, line drawings and outlines that were later remembered in comparison to correct rejections. For all three image types an old/new effect occurred between around 300 and 500 ms with a maximum over frontocentral electrode sites. In the latency region of interest, between 600 and 900 ms, the ERP old/new effects were widely distributed across the scalp for all three stimulus materials. In a later time region after around 900 ms the difference between remember and correct rejections showed its maximum over right frontal sites, again for all three image types (see Figure 20 for spline maps).

The statistical analyses confirmed those observations. Old/new effects were quantified by measuring the mean amplitude in three different latency regions: 300-500 ms, 600-900 ms and 900-1200 ms. These time intervals are consistent with those reported in previous ERP retrieval studies (Curran, 2000; Schloerscheidt & Rugg, 1997; Schloerscheidt & Rugg, 2004) and with those used in Experiment 2 in this Chapter. The analyses did not reveal any significant interactions with the gradation of the amount of perceptual information, old/new and sites in all three latency regions (300-500 ms: $p = .471$; 600-900ms: $p = .813$; 900-1200 ms: $p = .740$).

300-500 MS

In the first latency region, the analyses revealed a significant interaction between old/new and electrode site across the three image types ($F(3.6,64.7) = 8.71$, $p < .0001$). Subsidiary analyses with additional within subject factors location (anterior/posterior), hemisphere (left/right) and site (7,19,17,8,20,18,11,23,29,12,24,30) revealed an interaction between old-new and location irrespective of the image type ($F(1,18) = 9.75$, $p = .006$), indicating a larger old/new effect over anterior scalp sites (2.08 μV) than over posterior sites (1.03 μV).

600-900 MS

The ANOVA for the second time region between 600 and 900 ms resulted in a significant interaction between old/new and sites ($F(3.8,67.7) = 6.80$, $p < .0001$) irrespective of the gradation of the amount of pictorial information. This interaction remained significant after scaling the data ($F(3.8,67.9) = 6.80$, $p < .0001$). Subsidiary analyses on a selection of electrodes resulted in a significant interaction between old/new, location and hemisphere ($F(1,18) = 26.06$, $p < .0001$). Further analyses were conducted to understand the interaction, indicating a stronger effect over the left hemisphere over posterior scalp sites, although it just approached significance ($p = .050$) and a stronger effect over anterior sites over the right hemisphere ($F(1,18) = 8.26$, $p = .010$, 2.51 μV vs. 3.42 μV).

900-1200 MS

The ANOVA in the latency region from 900-1200 ms revealed also a significant interaction between old/new and electrode sites ($F(3.3,58.6) = 5.96$, $p = .001$).
The interaction remained significant after scaling the data ($F(3.3,59.2) = 6.03$, $p = .001$). Subsidiary analyses resulted in a significant interaction between old/new and hemisphere ($F(1,18) = 7.88$, $p = .012$), indicating a larger old/new effect over right sites (3.51 μV) than left locations (2.57 μV). Moreover, the analyses resulted in a significant interaction between old/new, location and hemisphere ($F(1,18) = 10.49$, $p = .005$). Subsidiary analyses indicate a larger old/new effect over right anterior electrodes (4.20 μV vs. 2.65 μV) than over left locations ($F(1,18) = 13.41$, $p = .002$; posterior sites $p = .349$).

In sum, images elicited a widespread old/new effect that was pronounced over left parietal and right anterior sites in the latency region of interest (600-900 ms) irrespective of the gradation of pictorial information.

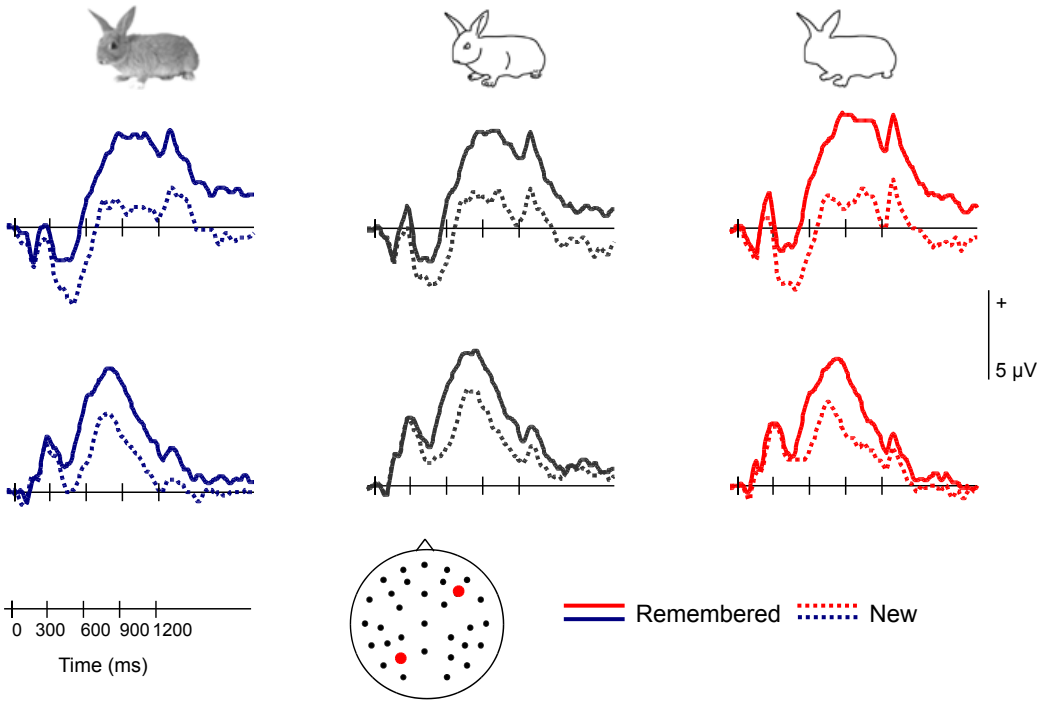

Figure 19. Retrieval-related neural activity. Group averaged ERP waveforms at test are compared for remembered (solid line) versus correct new responses (dotted line) for photographs, line drawings and outlines. The waveforms for two representative electrode sites (equivalent to LP and RF of the international 10/10 system) are displayed. Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes.

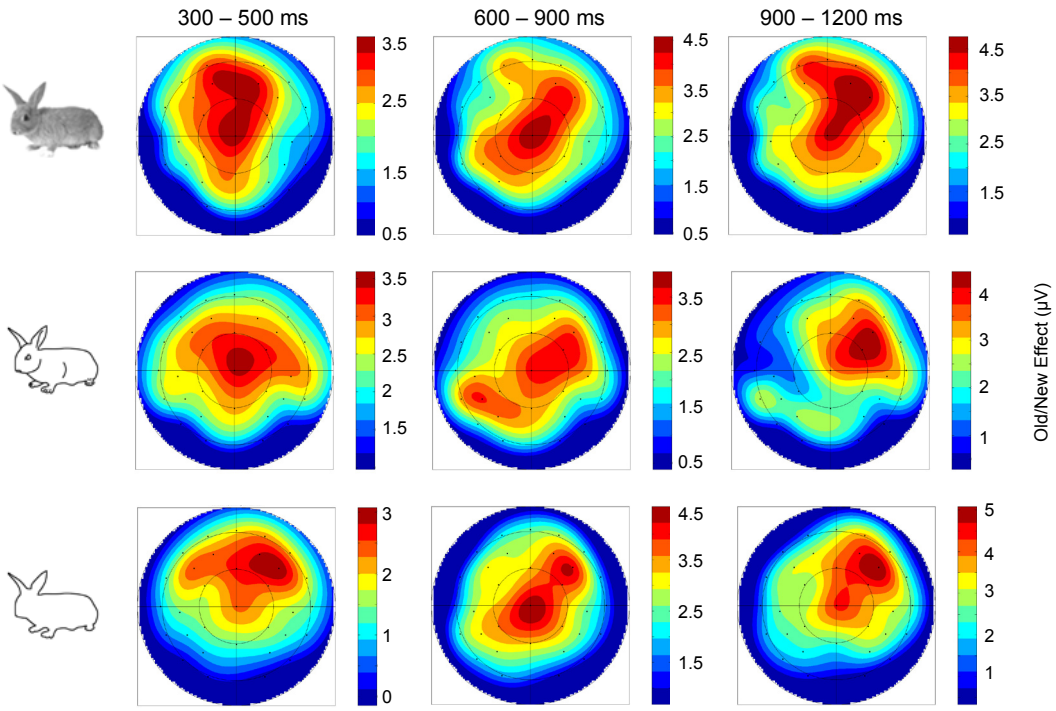

Figure 20. The spline maps illustrate the scalp distribution of the difference activity between remembered and correct new responses for photographs, line drawings and outlined in the latency region of 300-500 ms, 600-900 ms and 900-1200 ms.

3.2.4 DISCUSSION

The current experiment manipulated the degree of perceptual information from outlines, to more detailed line drawings and perceptually rich photographs to investigate whether retrieval-related brain activity grades with the degree of perceptual details.

Memory performance differed significantly depending on the amount of pictorial details. Memory for photographs was significantly better than for line drawings and outlines. A gradation in memory performance from outlines over line drawings and photographs was not found, because memory performance between outlines and line drawings did not differ. These behavioural findings suggest that the pure amendment of more pictorial details did not improve memory, but rather the addition of other types of perceptual features that were specific to photographs (e.g. depth and shade information).

Concerning the ERP data it was hypothesised that the old/new effect in the latency region that is usually associated with recollection processes grades with the amount of perceptual information. However, the old/new effect unexpectedly did not differ depending on the amount of perceptual details. Irrespective of the image type, the old/new effect was widely distributed and pronounced over left-parietal and right anterior locations.

These findings did not resemble the material-specific retrieval effects reported in the previous literature. Those studies reported left-parietal old/new effects for line drawings (Curran & Clearly, 2003) and words (e.g. Schloerscheidt & Rugg, 1997) and more right anterior old/new effects for photographs of faces and objects (Galli & Otten, 2010; Yick & Wilding, 2008). Interestingly, the dissociation between a left-parietal effect and a more right anterior effect for outlines and photographs respectively that was observed in Experiment 2 could not be replicated here. The old/new effects in the present experiment were more widely distributed than for outlines and photographs in Experiment 2. However, a direct comparison between both experiments and in turn a functional interpretation in those lines is difficult due to differences in the experimental designs.

The absence of distribution differences as a function of the amount of pictorial information might be related to differences in the experimental designs between the current experiment and Experiment 2. The current experiment contained only a subset (approximately 50%) of the images used in Experiment 2. This might have affected the degree of difficulty of the memory test. Overall memory performance was considerably higher in the current experiment (photographs: 90%; outlines: 73%) than in Experiment 2 (photographs: 65%; outlines: 60%). Besides the reduction of trials, the differences in difficulty between both experiments might have been also related to the manipulation of study-test congruency in Experiment 2. In Experiment 2 half of the studied outlines and photographs were presented in the alternative presentation mode at test. In contrast the presentation mode did not change between study and test in the current experiment. Therefore, the discrimination between old and new items might have been easier overall in the current experiment than in Experiment 2. The study-test congruency manipulation in Experiment 2 might have induced a greater focus on perceptual features of the test items. To confidently remember an object that might have been initially encountered in the alternative mode, participants most likely had to be also certain about the presented image type and therefore had to engage to a greater extent perceptual processing strategies in Experiment 2. The stronger focus and salience of perceptual features at test in Experiment 2 may be associated with the difference in ERP effects depending on the image type relative to the current experiment. Here, the presentation mode between study and test did not change at retrieval. Therefore, the perceptual features across the image types might have been less salient. Recollection processes may have been based predominantly on other distinct attributes such as conceptual details than on perceptual information. Therefore, the three different kinds of image types were possibly less discriminative and, in turn, processed more perceptually homogenously at retrieval.

In line with the previous interpretation participants reported that they were not aware that the items were presented in their mirror-reversed version in the current experiment. In contrast, in Experiment 2 participants consistently noticed and recollected perceptual changes such as the mirror-reversed orientation of the test items. This observation is consistent with the speculation that participants in Experiment 2 may have been focused on the perceptual features of the test items which might in turn have led to distinct retrieval processes as a function of the amount of pictorial information. Therefore it may be possible that the dissociation between left-parietal and right frontal effects is not per se dependent on the amount of perceptual details, but may be also influenced by the type of processing focus at retrieval. Only when the perceptual features are of relevance or salience at test, retrieval-related brain activity may differ depending on the image type. For instance, in MacKenzie and Donaldson (2009) perceptual feature processing was most likely also of some relevance at retrieval. While at study, faces and names were presented, at test only either faces or name cues were used as probes. Also here not the entire studied content was used as probe at test which might have increased the salience of the perceptual features.

These interpretations are based on speculations and further research and direct comparisons within one experiment are needed. For instance, in future studies the degree of perceptual salience (e.g. study-test manipulation) could be manipulated across blocks or groups to elucidate its effects on retrieval-related brain activity.

Together, the experiments in Chapter 3 demonstrated that recollection-related brain activity does not vary with the mere perceptual overlap, but differs qualitatively with the amount of perceptual information of the retrieval cue. However, the perceptual specificity of recollection-related brain activity may not be a universal organizational principle of neural correlates of long-term memory. For instance the salience of the perceptual attributes may be a mediating factor.

CHAPTER 4 : NEURAL REINSTATEMENT AS REVEALED BY OSCILLATORY THETA ACTIVITY

4.1 INTRODUCTION

According to neural models of episodic memory, memory retrieval depends on the reinstatement of brain activity patterns that were initially engaged at encoding (e.g. Norman & O'Reilly, 2003; Rolls, 2000). Recent event-related fMRI findings show initial evidence that encoding-related activity overlaps with the neural correlates of retrieval (Johnson et al., 2009; Johnson & Rugg, 2007; Kahn et al., 2004; Vayda et al., 2002; Wheeler et al., 2006). However, due to the low temporal resolution of the hemodynamic brain signals it is not clear whether reinstatement effects are directly related to successful recollection or represent processes that are rather a consequence of the recovery of episodic information, such as post-retrieval processes (for review see Rugg et al., 2008). Therefore, methods with higher temporal resolutions such as EEG or MEG are required.

A recent ERP study investigated the temporal characteristics of reinstatement effects (Johnson et al., 2008). However, they were only focused on the retrieval-related ERPs. The authors reported content-dependent differences in recollection–related ERPs over anterior locations starting as early as recollection-related effects are usually expected. Recollected words that were studied in a sentence generation task were associated with frontally distributed recollection effects and words that were encoded in an imagery task were associated with a left-parietal ERP old/new effect. Although there are initial attempts to look at neural reinstatement with ERPs, as yet studies only investigated indirect neural overlap, because ERPs were only recorded and analysed at retrieval. Still, there are methodological issues that need to be overcome to assess the neural reinstatement across encoding and retrieval-related ERPs (cf. Johnson et al., 2008; Norman et al, 2006).

The examination of brain oscillations provides the possibility to investigate neural reinstatement. The overlap between encoding- and retrieval-related brain oscillations in a specific frequency band may benefit memory. Scalp and intracranially recorded EEG and MEG findings show consistent evidence that oscillatory activity in the theta frequency band (4-8 Hz) plays a relevant role in memory functions (for review see Düzel et al., 2010; Nyhus & Curran, 2010). Although it is controversial to assume that a specific frequency band is unique to a specific cognitive function (Klimesch et al., 2008; Nyhus & Curran, 2010), EEG and MEG studies provided evidence that theta oscillations are associated with encoding and retrieval processes of episodic memories (for review see Düzel et al., 2010; Klimesch et al., 2008; Nyhus & Curran, 2010). Furthermore, there is consistent evidence that theta oscillations may be associated with control processes and top-down processes in working memory and episodic memory (Kahana, Seelig & Madsen, 2001; Khader, Jost, Ranganath & Rösler, 2010; Klimesch, 1999; Mecklinger, Kramer & Strayer, 1992; Sauseng, Klimesch, Schabus & Doppelmayr, 2005).

At encoding, studies using words as stimulus material reported a larger theta power increase for later remembered than forgotten items (Caplan & Glaholt 2007; Hanslmayr et al., 2008; Khader et al., 2010; Klimesch, Doppelmayr, Russegger & Pachinger, 1996; Moelle et al., 2002; Sederberg et al., 2003; 2007; Summerfield & Mangels 2005). To my knowledge there is only one study that used pictures as stimulus material to study encoding-related theta power effects. Osipova et al. (2006) reported a theta power increase for later remembered relative to forgotten pictures. Together, these findings suggest that theta oscillations play an important role in memory formation (for review see Nuyhus & Curran, 2010).

At retrieval, frontal theta power has been found to be larger for hits than correct rejections in word and picture recognition tests (Burgess & Gruzelier, 1997; Düzel et al., 2003; Düzel, Neufang & Heinze, 2005; Gruber, Tsivilis, Giabbiconi & Müller 2008; Klimesch, Doppelmayr, Stadler, Pöllhuber, Sauseng & Röhm, 2001; Osipova et al., 2006; Summerfield & Mangels, 2005). Moreover, theta power increase has been associated with the successful retrieval of source information (Addante, Watrous, Yonelinas, Ekstrom & Ranganath, 2011; Gruber et al., 2008; Guderian & Düzel, 2005). In the same vein, studies using R/K paradigms have demonstrated that items that were later correctly remembered were selectively associated with a theta increase (Klimesch et al., 2001; Summerfield & Mangels, 2005). Together, these

findings indicate that theta oscillations at retrieval play a role in the recollection of episodic information.

In this Chapter the encoding and retrieval data of Experiment 2 were reanalysed in the frequency domain to investigate whether oscillatory theta power is influenced by encoding-retrieval overlap. Experiment 2 provides a good possibility to investigate neural reinstatement, because Experiment 2 investigated study-test congruency within-subjects and demonstrated robust study-test congruency effects for both types of perceptual information. The reanalysis of Experiment 2 in the frequency domain assessed whether the amount of perceptual information at study or test influences oscillatory power in the theta frequency band during encoding and retrieval. The amount of perceptual information was varied at study and test and items were either probed in the same presentation mode (outlines-outlines; photographs-photographs) or the alternative mode of presentation (outline-photograph, photograph-outline) at test. The research question was based on the assumption that the neural correlates of recollection may be content-dependent and may reflect the reinstatement of processes that were initially engaged during encoding (e.g. O'Reilly & Norman, 2003; Rolls, 2000). If theta power plays a role for the reinstatement of encoded context, theta power was expected to be present over similar scalp locations at encoding and retrieval as a function of the amount of perceptual overlap.

4.2 METHODS

The information regarding participants, materials, procedure and EEG acquisition have already been described in Experiment 2 of Chapter 2. Because the analysis was focused on encoding-related and retrieval-related activity the same participants (N=19) as described in Experiment 2 in Chapter 2 were used for the time-frequency analysis of the study and test data.

EEG TIME-FREQUENCY ANALYSIS

The pre-processing steps of applying offline filters and the segmentation of the continuous EEG data were executed in *Neuroscan*. The analysis procedure resembles to a great extent the analysis method used in Addante et al. (2011) and Gruber, Watrous, Ranganath, Ekstrom and Otten (in preparation). The continuous EEG data were high-pass filtered with a cut-off point of 0.5 Hz. This pre-processing step removed slow drifts which is necessary for the independent component analysis (ICA) that was carried out in a later analysis step. The EEG data at encoding and retrieval were segmented into epochs that extended from -800 to 2.1 sec. This epoch length ensured that time-frequency information could be extracted from -200 ms before until 1.5 sec after stimulus onset without contaminations by edge effects at the beginning and end of the epoch. The following analysis steps were conducted with Matlab 7.8 (MathWorks) and the EEGlab toolbox (Delorme & Makeig, 2007). To remove muscle artefacts and other non-biological artefacts, trials were rejected when they contained EEG activity that exceeded three standard deviations from the mean at a specific electrode or more than five standard deviations of the mean across all electrodes. Based on ICA decompositions, components were excluded that contained blinks and eye movement artefacts (Bell & Sejnowski, 1995; Delorme & Makeig, 2004). In the next step, trials that were still contaminated by artefacts such as amplifier saturation or muscle tensions were manually rejected. After the artefact rejection, the data were re-referenced to the average of the left and right mastoid electrodes.

Spectral decomposition was then executed on the pre-processed data using Morlet wavelets (Perceival & Walden, 1993). The previous literature has consistently shown that wavelets estimate oscillatory power with a good spectral and temporal resolution (e.g. Van Vugt et al., 2007). The spectral power computation was conducted in 1 Hz steps in the frequency range of 4 Hz to 12 Hz (Niedermeyer, 2005). The analysis was conducted with four cycles with a sliding time window of 20 ms between -200 ms and 1.5 sec. The frequency power was baseline corrected to the average frequency power in the time window from -200 to -100 ms before item onset via a subtraction approach for each frequency (4-12 Hz) across each data point of the epoch (Hanslmayr, Leipold, Pastötter & Bäuml, 2009; Pastötter, Schicker, Niedernhuber & Bäuml, 2011). Time-frequency power at encoding was averaged according to remember and forgotten responses (studied items that were later rejected as new

item) for each of the four conditions (photograph-photograph, photograph-outline, outline-outline, outline-photograph). For the retrieval data time-frequency power was similarly averaged according to study-test congruency, the amount of pictorial information and according to whether participants remembered the item correctly and whether the item was correctly judged as new (old/new effect). For the encoding analyses the mean number of trials (range) of remember responses for studied outlines and photographs in the match and mismatch condition were 33 (21-49), 36 (17-48), 26 (14-45) and 24 (16-45). The mean number of trials of forgotten responses to the corresponding conditions were 29 (15-44), 38 (21-57), 27 (16-45) and 39 (26-56). For the retrieval analyses the mean number of trials of remember responses for outlines and photographs in the match and mismatch conditions were 34 (22-50), 39 (16-51), 26 (14-50) and 27 (15-44). The mean number of trials of correct new responses for outlines and photographs were 63 (21-82) and 68 (50-81).

STATISTICAL ANALYSES

In order to statistically test whether theta power (4-8Hz) at encoding is influenced by study-test congruency and amount of pictorial information repeated measures ANOVAs were conducted. These analyses incorporated the within-subject factors study-test congruency (congruent/incongruent), perceptual information (outlines/photographs), subsequent memory (remember/forgotten) and site (32 electrodes, see Figure 3 for montage). Reliability of theta power at retrieval across participants was similarly tested, but instead of subsequent memory the factor old/new (remember/correct rejection) was used. ANOVAs are commonly used as statistical analysis methods in the field of time -frequency analysis (e.g. Hsieh, Ekstrom & Ranganath, 2011; Khader et al., 2010; for other analysis methods see Maris & Oostenveld, 2007). Only effects incorporating subsequent memory or old/new are reported. Significant interactions were followed by subsidiary analyses to understand the nature of the effect. Greenhouse-Geisser corrected df and p-values are reported to account for possible violations of the sphericity assumption (Keselman & Rogan, 1980).

4.3 RESULTS

The behavioural performance for the study and test phase of the 19 participants that were included in the time-frequency analysis has already been described in Experiment 2 of Chapter 2.

ENCODING-RELATED THETA POWER EFFECTS

Figure 21 and Figure 22 display the time-frequency representations (TFRs) for a representative left frontal electrode for encoded outlines and photographs that were later probed with a congruent or incongruent cue. Figure 21 and Figure 22 also show the corresponding spline maps displaying the distribution of the subsequent memory effect (i.e. remember-forgotten) across the scalp. Encoded photographs were associated with encoding-related theta power (i.e. subsequent memory effect) increase irrespective of the congruency of the test probe. In contrast, encoded outlines did not elicit encoding-related theta power increases. The statistical reliability of the mean theta power across participants was quantified within the latency region of 200 and 600 ms after item onset. The latency region was chosen based on visual inspection and incorporated the largest visible effects for each of the four conditions.

Statistical analyses confirmed this observation. An initial ANOVA revealed a significant interaction between the encoded amount of pictorial information, subsequent memory and site ($F(5.5,99.1) = 5.09$, $p < .0001$). While the separate analysis of encoded photographs resulted in a significant interaction between subsequent memory and site ($F(4.9,88.9) = 4.64$, $p = .001$), outlines did not reveal a significant subsequent memory effect ($p = .993$) or an interaction with site ($p = .409$). A subsidiary analysis on the subset of six left frontal electrodes (18, 33, 34, 50, 48, 49, see Figure 3 for montage), where the effect was maximal, was conducted to understand the topography of the theta power increase for encoded photographs. The ANOVA revealed a significant subsequent memory effect ($F(1,18) = 7.40$, $p = .014$).

Together, the analysis on the encoding data revealed a significant left frontopolar encoding-related theta power increase that was specific to the encoded amount of pictorial information. This effect was only evident for perceptually rich photographs and did not vary with the nature of the test probe.

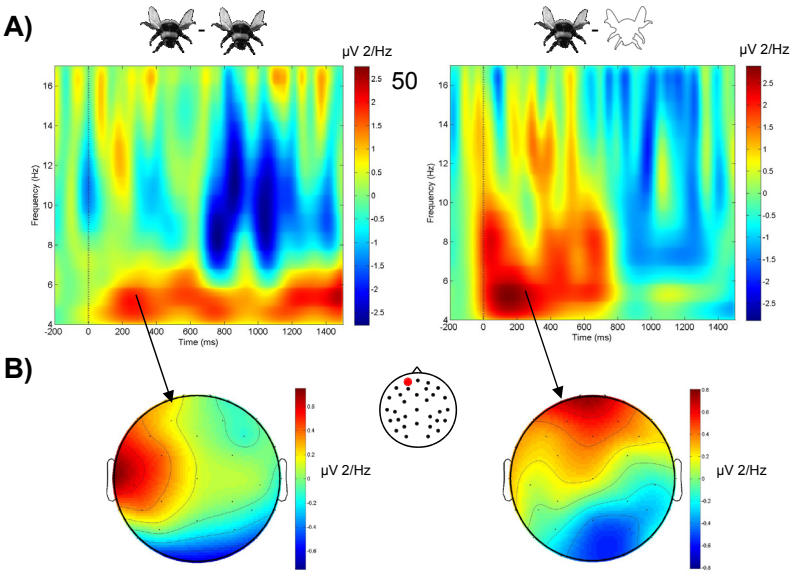

Figure 21. Encoding-related theta power for studied photographs. A) Time-frequency representations of encoding-related theta activity (i.e. theta power for subsequently remembered items minus theta power of later forgotten items) at one representative electrode of the frontal cluster (electrode 50, see Figure 3 for montage) that showed a statistical significant theta power effect for photographs that were cued with the congruent probe (left) and incongruent cue (right). Time-frequency computations were conducted in 1 Hz steps. The time frequency representations were smoothed for visual purposes. Encoded photographs (left and right) showed both an encoding-related theta increase between approximately 200 and 600 ms. B) The scalp maps display the difference in theta power between subsequently remembered and later forgotten photographs in the congruent (left) and incongruent condition (right) in the time window of 200 and 600 ms after the onset of the photograph.

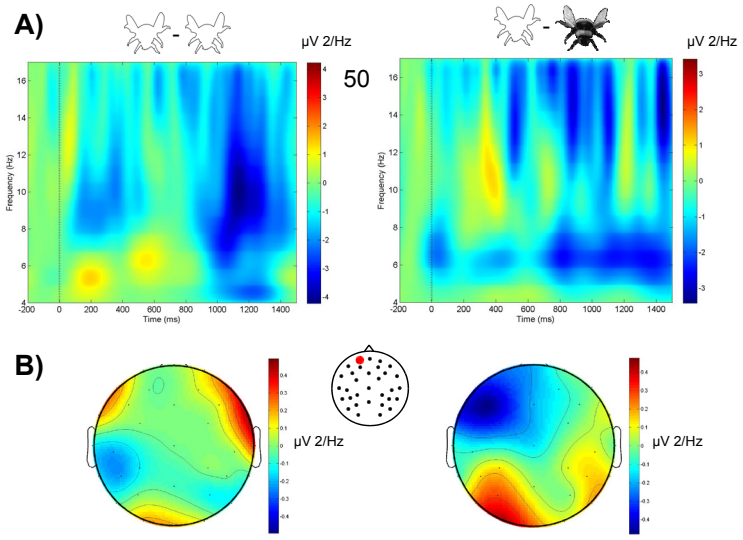

Figure 22. Encoding-related theta power for studied outlines.
A) Time-frequency representations of encoding-related theta activity (i.e. theta power for subsequently remembered items minus theta power of later forgotten items) at one representative electrode of the frontal cluster (electrode 50, see Figure 3 for montage) for outlines that were cued with the congruent probe (left) and incongruent cue (right). Time-frequency computations were conducted in 1 Hz steps. The time frequency representations were smoothed for visual purposes. Encoded outlines (left and right) did not show an encoding-related theta increase. B) The scalp maps display the difference in theta power between subsequently remembered and later forgotten outlines in the congruent (left) and incongruent condition (right) in the time window of 200 and 600 ms after the onset of the outline.

RETRIEVAL-RELATED THETA POWER EFFECTS

In Figures 23 and 24, TRFs for one fronto-central and one left-parietal electrode site are displayed for photographs and outlines in the congruent and incongruent conditions. Figures 23 and 24 also show the corresponding spline maps. For both encoded photographs and outlines theta-related retrieval effects were evident (i. e. old/new effect). However, for encoded photographs this theta power increase was more distributed over frontal sites. Encoded outlines instead showed a retrieval-related theta increase over left-parietal locations.

Statistical analyses incorporated the mean theta power in the latency region of 400-800 ms. Again, the time window was chosen based on visual inspection. Moreover, this time region is usually associated with recollection-related brain activity (e.g. Klimesch et al., 2001). The statistical analyses confirmed the observations. An initial ANOVA revealed a significant interaction between encoded amount of perceptual information, old/new and site ($F(5.2,93.6) = 3.89$, $p = .003$). A subsidiary analysis on seven anterior (34, 18, 8, 21, 10, 33, 22) and seven posterior electrodes (14, 12, 16, 29, 26, 30, 25) was carried out to understand the nature of the interaction. The analysis revealed a significant interaction between the encoded amount of pictorial information, old/new and location (anterior/posterior) ($F(1,18) = 7.21$, $p = .015$). Significant differences in the old/new effect as a function of the encoded amount of information was evident only at anterior scalp electrodes ($F(1,18) = 9.24$, $p = .007$, posterior $p = .526$). Only for photographs a significant retrieval-related theta increase was found over anterior locations ($F(1,18) = 18.58$, $p < .0001$; other $ps > .288$).

Encoded photographs elicited a retrieval-related theta effect that was widely distributed (old/new effect $F(1,18) = 13.42$, $p = .002$) including frontal locations. In contrast, encoded outlines were associated with a significant interaction with old/new and sites ($F(3.0,54.4) = 2.30$, $p = .040$). Subsidiary analyses demonstrated a maximum over left-parietal locations (see Figure 24).

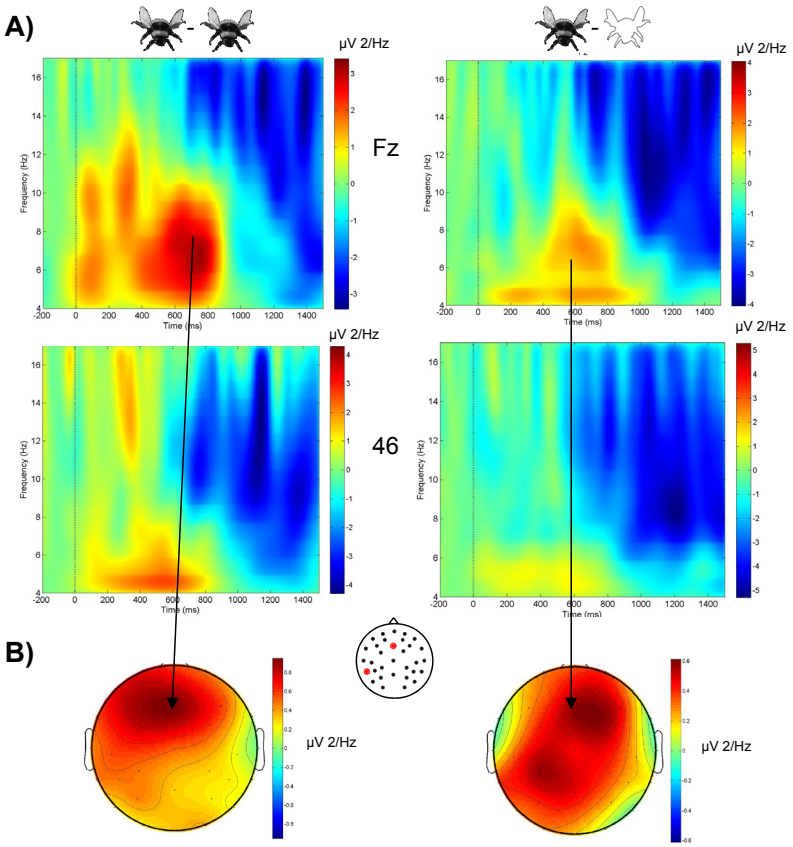

Figure 23. Retrieval-related theta power for encoded photographs
A) Time-frequency representations of retrieval-related theta activity (i.e. theta power for remembered items (hits) minus unstudied items that were correctly rejected as new) for photographs (left) and outlines (right) that were previously encoded as photograph. Displayed are time-frequency representations of a representative electrode of the frontal cluster (Fz, see Figure 3 for montage) and a parietal electrode (46, see Figure 3 for montage) of the posterior electrode cluster that were used in the statistical analysis. Time-frequency computations were conducted in 1 Hz steps. The time frequency representations were smoothed for visual purposes. Encoded photographs (left and right) showed both a retrieval-related theta increase between approximately 400 and 800 ms widespread across the scalp irrespective of the retrieval cue. B) The scalp maps display the difference in theta power between remembered and correct rejected new items in the congruent (left) and incongruent condition (right) in the time window of 400 and 800 ms after the onset of the photograph test cue (left) and outline retrieval cue (right).

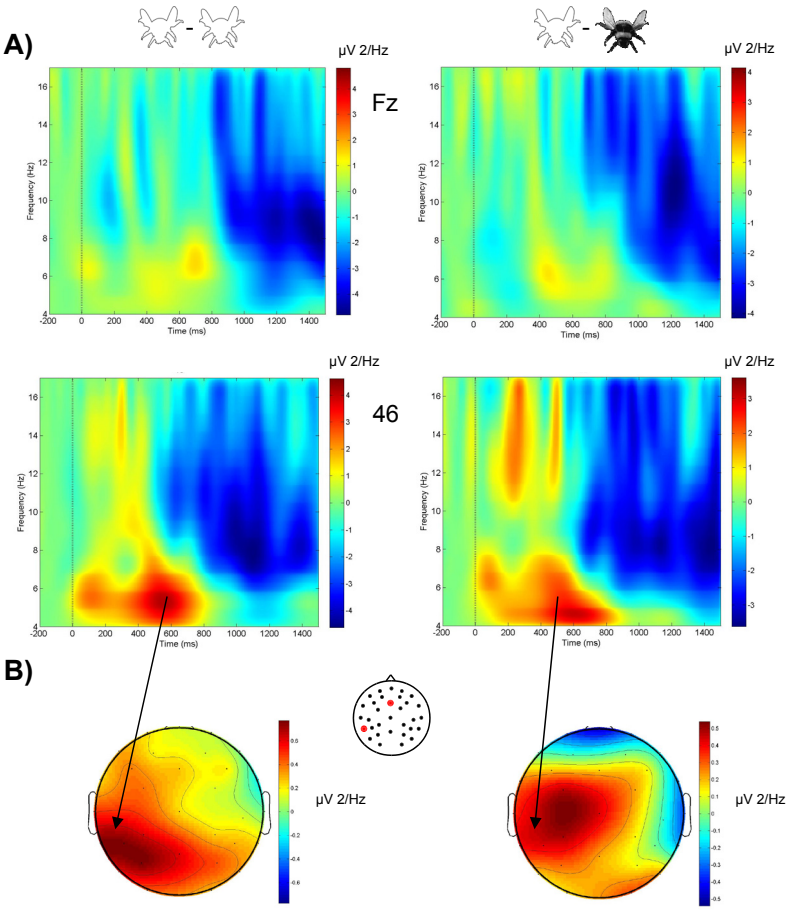

Figure 24. Retrieval-related theta power for encoded outlines
A) Time-frequency representations of retrieval-related theta activity (i.e. theta power for remembered items (hits) minus unstudied items that were correctly rejected as new) for encoded photographs (left) and outlines (right) that were initially encoded as outline. Displayed are time-frequency representations of a representative electrode of the frontal cluster (Fz, see Figure 3 for montage) and a parietal electrode (46, see Figure 3 for montage) of the posterior electrode cluster that were used in the statistical analysis. Time-frequency computations were conducted in 1 Hz steps. The time frequency representations were smoothed for visual purposes. Encoded outlines (left and right) showed a retrieval-related theta increase between approximately 400 and 800 ms pronounced over left parietal scalp locations irrespective of the retrieval cue. B) The scalp maps display the difference in theta power between remembered and correct rejected new items in the time window of 400 and 800 ms after the onset of the photograph test cue (left) and outline retrieval cue (right) that were initially encoded as outline.

CORRELATION BETWEEN THETA POWER AT ENCODING AND RETRIEVAL

Because encoded photographs were associated with a theta power increase over frontal sites at both encoding and retrieval, a bivariate correlation was conducted between participants' mean encoding-related theta power for later remembered responses relative to the baseline and their mean theta power at retrieval. The mean theta power for each participant at encoding and retrieval was averaged across the significant cluster of frontal electrodes in the time window of 200-600 ms at encoding and the significant frontal electrode cluster at retrieval of 400-800 ms after item onset. Frontal theta power increase for remembered responses at encoding correlated significantly with frontal theta power increase at retrieval (Pearson's r = .692, p = .001). The correlation was positive, indicating that participants who showed a frontal theta increase at encoding showed a larger frontal theta increase at retrieval (see figure 4).

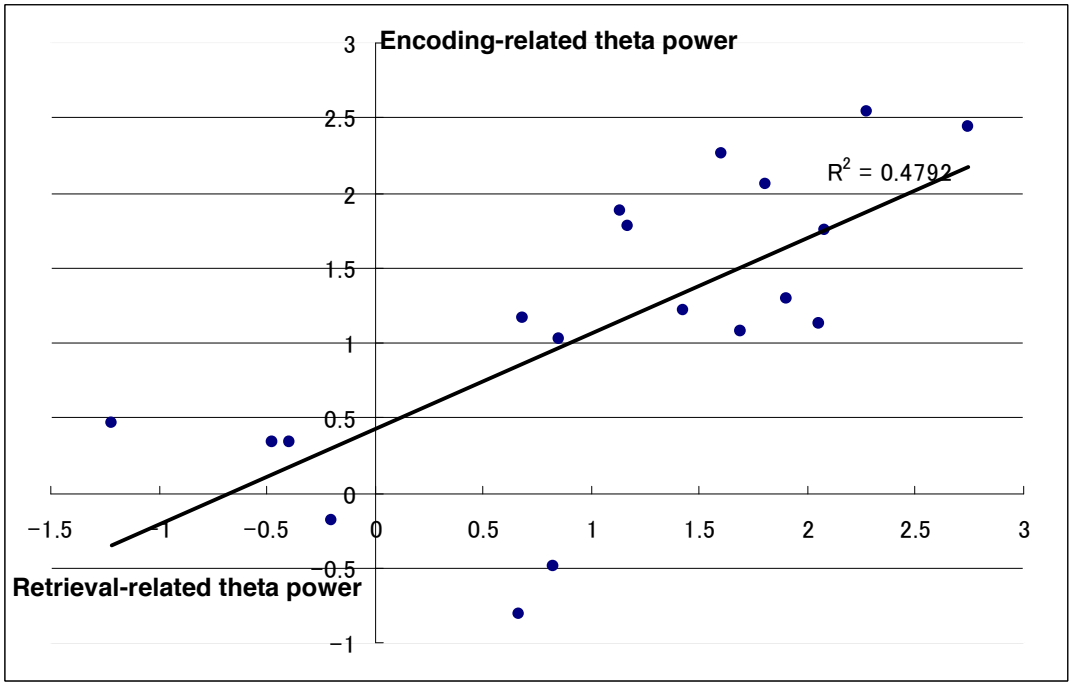

Figure 25. Correlation between theta power increase at encoding and retrieval.

4.4 DISCUSSION

The question of interest was whether the amount of perceptual information at encoding and retrieval affects encoding-related and retrieval-related theta effects. The amount of perceptual information was manipulated by presenting perceptually impoverished outlines and photographs at study and test. Half of the test items were presented in the same presentation mode as during study and half were cued in the alternative presentation mode. Both encoding-related and retrieval-related theta power were influenced by the encoded amount of perceptual information. For perceptually rich items, frontal theta increased during encoding as well as at retrieval. This was evident irrespective of the type of test probe. In contrast, encoded outlines did not show an increase in theta power at encoding. At retrieval, encoded outlines were associated with a theta increase over left temporal-parietal scalp sites.

The fact that frontal theta increase is specific to perceptually rich pictures at both encoding and retrieval may indicate the reinstatement of encoded perceptual information. The positive correlation between the frontal encoding and retrieval-related theta increase for photographs may support this interpretation. This would be in line with the neural models of episodic memory (Norman & O'Reilly, 2003; Rolls, 2000) that state that memory benefits from the reinstatement of processes that were initially engaged at encoding. Photographs may involve to a greater extent perceptual analysis processes in comparison to outlines. The successful retrieval of perceptually richer photographs may rely on the recovery of perceptual details. In turn, encoded photographs are subsequently successfully remembered when those encoded perceptual attributes are reinstated (cf. Galli & Otten, 2010; Yick & Wilding, 2008). Thus, the retrieval-related theta effect over frontal locations for encoded photographs may reflect the reinstatement of perceptual processes.

It may not be surprising that an encoding-related theta increase was evident over frontal locations, because previous studies using iEEG and MEG provided evidence that frontal theta increase may be associated with top-down control processes to incorporate information in episodic memories (cf. Nyhus & Curran, 2010; Klimesch et al., 1996; Sederberg et al., 2007; Summerfield & Mangels, 2005). The encoding and retrieval of a greater amount of perceptual information may be associated with the engagement of more control processes to encode and retrieve perceptual information.

As yet, it is not clear how the scalp distribution of encoding-related theta power is modulated. For instance one other study that used pictures demonstrated a parietal encoding-related theta effect (Osipova et al., 2006). The topographical differences to the current experiment may be related to the various differences in the experimental designs such as the type of images that were used (objects versus landscapes and buildings), the type of encoding task (incidental versus intentional encoding task) and the type of recognition tasks (R/K paradigm versus old/new confidence judgements).

However, the majority of the studies using words reported consistently increases in encoding-related theta power activity over frontal locations (Hanslmayr et al., 2008; Moelle et al., 2002; Sederberg et al., 2003; Summerfield & Mangels, 2005). Interestingly a recent study comparing encoding-related oscillatory power across two types of encoding tasks (i.e. deep or semantic encoding strategy versus shallow or perceptual encoding task) reported encoding-related theta increases only for words that were initially encoded in the shallow encoding task that was focused on the physical features (Hanslmayr et al., 2008). These findings are in line with the interpretation of the oscillatory findings in my PhD thesis which suggest that theta oscillatory activity may reflect perceptual analyses processes that are used to incorporate the incoming information in episodic memory traces.

At retrieval, frontal retrieval-related theta increase has been demonstrated in several studies (Addante et al., 2011; Burgess & Gruzelier, 1997; Düzel et al, 2005; Klinesch et al., 1996) and has been also associated with top-down control processes that lead to retrieval of associative memory representations (Kahana et al., 2001; Klimesch et al., 2008; Polyn & Kahana, 2008). Furthermore, the findings are consistent with three studies that show that theta power increase over frontal sites is associated with the recollection of specific details of the studied episode (Addante et al., 2011; Gruber et al., 2008; Guderian & Düzel, 2005).

Interestingly, the frontal-theta increase for photographs is consistent with previous ERP findings that compared the recollection-related ERP effects across different stimulus categories (Galli & Otten, 2010; MacKenzie, 2009; Yick & Wilding, 2008). Information that contained more perceptual information such as faces and objects were associated with more frontal contributions than words. Although the neural sources of an effect are difficult to determine with EEG (Nuñez, 1981), fMRI findings have demonstrated that anterior regions may be associated with the recovery of encoded context (Rugg et al., 1999).

But why is the reinstatement of encoding processes specific to photographs and how are outlines remembered? Consistent with previous findings (Addante et al., 2011, Klimesch 2008) both encoded outlines and photographs were associated with parietal theta increases. Because of the parietal distribution of the retrieval-related theta effect and its temporal occurrence (400-800 ms) this effect has been directly linked to the left-parietal ERP effect that is usually seen as a generic index of recollection (Addante et al., 2011). Because outlines contain a minimum of perceptual information the reinstatement of perceptual details and a frontal theta power increase may not be evident. Therefore, the frontal retrieval-related theta effect may be related to the reinstatement of perceptual details.

An alternative possibility is that the frontal retrieval-related theta increase for encoded photographs reflects post retrieval processes such as retrieval monitoring and evaluation of the retrieved content (Blumenfield & Ranganath, 2007). However, the early occurrence of this effect is inconsistent with these interpretations, because effects reflecting post retrieval processes do not usually occur before 800 ms after stimulus onset (Blumenfield & Ranganath, 2007; Wilding & Rugg, 2000). The early occurrence of frontal theta effects is more in line with the interpretation that the underlying processes are related to the direct recovery of episodic information (Yick & Wilding, 2008).

Future studies with higher spatial resolution such as MEG in combination with methodological approaches such as multivariate pattern classification may help to provide deeper understanding of the role of theta oscillations in the reinstatement of processes across encoding and retrieval and help to pinpoint its neural generators. For instance, a recent MEG study applied a multivariate pattern classification approach to a working memory paradigm and demonstrated that the reinstatement of theta oscillations plays an important role in working memory maintenance (Fuentemilla, Penny, Cashdollar, Bunzeck & Düzel, 2010)

Together, the current findings demonstrate that frontal theta increase at both encoding and retrieval is specific to the perceptual details at encoding. The present study provides support for the reinstatement models, because theta increased over frontal sites at encoding and retrieval selectively for encoded photographs. Frontal theta increase may play an important role for the reinstatement of encoded content (cf. Nyhus & Curran, 2010; Polyn & Kahana, 2008).

CHAPTER 5: GENERAL DISCUSSION

My PhD research aimed to elucidate how the similarity between encoding and retrieval operations influences neural correlates of human long-term memory. Four EEG experiments were conducted to address this question. The impact of the interdependence between encoding and retrieval processes on episodic memory has been stressed in cognitive frameworks and neurocomputational models (e.g. Norman & O'Reilly, 2003; Roediger, 1990). In line with those theories, behavioural studies have consistently demonstrated that memory benefits from an overlap of encoding and retrieval processes (e.g. Blaxton, 1989; Morris et al., 1977). However, thus far little is known about how the interplay between encoding and retrieval processes affect the neural correlates of human long-term memory. Therefore, my PhD addressed the following three main research questions: 1) Does encoding-related activity vary with the similarity of cognitive operations between encoding and retrieval? 2) Does the amount of perceptual information across encoding and retrieval affect the neural correlates of retrieval? 3) Does oscillatory theta power activity play a role in the reinstatement of encoding processes? The following section summarises the main findings of the three research questions and place them into context with the previous literature. This is followed by discussing possible implications and future research directions.

5.1.2 DOES ENCODING-RELATED BRAIN ACTIVITY VARY WITH THE SIMILARITY OF COGNITIVE OPERATIONS BETWEEN ENCODING AND RETRIEVAL?

Three EEG experiments were conducted to investigate whether the similarity between cognitive processes at encoding and retrieval influences encoding-related ERPs. Experiment 1 addressed whether encoding-related ERPs differ as a function of the study-test congruency of mode of presentation. Experiment 2 asked whether the amount of perceptually richness and the study-test congruency influences encoding-related ERPs. Finally, in Experiment 3 the question was addressed whether encoding-related brain activity differs as a function of the type of processes that are emphasised at test (i.e. conceptual or perceptual processes).

Experiment 1 manipulated the congruency of the presentation mode between encoding and retrieval (i.e. word-word, word-picture, picture-picture, picture-word) to elucidate how the degree of overlap between encoding and retrieval affect the neural correlates of encoding. As expected and in line with the previous literature overall memory performance was better for items that were probed with the congruent cue (i.e. word-word; picture-picture) than with the incongruent cue (i.e. picture-word; word-picture) (e.g. Mintzner & Snodgrass, 1999; Mulligan & Osborn, 2009; Park & Rugg, 2008).

Crucially, encoding-related ERPs differed qualitatively as a function of the study-test congruency of mode of presentation. Because ERP analyses were restricted to remembered responses, it may be suggested that encoding-retrieval overlap plays a role in encoding-related brain activity predicting later recollection of episodic information. Interestingly, according to the findings in Experiment 1 the study-test congruency plays a role for only some item types and not others. Encoded words showed a subsequent memory effect over frontal locations irrespective of the study-test congruency. While encoded pictures that were later cued with a picture were associated with a subsequent memory effect over frontocentral locations, encoded pictures that were subsequently probed with words elicited a subsequent memory effect pronounced at posterior scalp electrodes. Therefore, it was concluded that different underlying processes may be associated with studied items later probed with a congruent and incongruent cue. According to the premise of the transfer appropriate processing framework the encoding-related processes reflect most likely those operations that overlap with the retrieval cue to support successful memory retrieval (for review see Roediger et al., 2002).

Experiment 1 demonstrated that encoding-retrieval overlap plays an important role for the neural correlates of encoding (see also Park & Rugg, 2008). Crucially, the use of an acquisition technique that has a high temporal resolution provided the possibility to determine whether the impact of encoding-retrieval overlap is directly related to the formation of memory representations or is rather a consequence of the encoding of the incoming information. The early onset of the modulation as a function of study-test congruency indicates that the similarity between encoding and retrieval processes plays a direct role in episodic memory encoding. Together, the findings in terms of the temporal characteristics of the encoding-retrieval overlap effect add important insights to the previous literature (Park & Rugg, 2008).

Based on the material-specific study-test congruency effects in Experiment 1, it was suggested that the amount of perceptual information might modulate the study-test congruency effects on the neural correlates of encoding. Therefore, Experiment 2 attempted to elucidate whether the engagement of perceptual analysis processes and the similarity between those operations across study and test affect the neural correlates of encoding. The emphasis of perceptual processes at encoding and retrieval was operationalised by either presenting perceptually rich photographs or perceptually impoverished outlines. As expected overall memory performance benefited from the perceptual match of mode of presentation. In line with Experiment 1, study-test congruency influenced the neural correlates of encoding. Both encoded outlines and photographs that were probed in the same mode of presentation elicited a frontally distributed subsequent memory effect. In contrast, encoded outlines and photographs that were probed with the alternative mode of presentation were associated with more widespread and posteriorly distributed subsequent memory effects. Based on the findings in Experiment 1, it was suggested that the amount of perceptual information might modulate the study-test congruency effects on the neural correlates of encoding. Indeed, the previous literature showed evidence for stronger study-test congruency effects for items that contained more perceptual information (e.g. Ecker & Zimmer, 2007; Schloerscheidt & Rugg, 2003). However, Experiment 2 showed evidence for qualitatively different subsequent memory effects as a function of study-test congruency irrespective of the amount of pictorial information a picture contained.

Together, the findings from Experiment 1 and 2 may indicate that the dissociation between frontally distributed effects and posteriorly distributed effects as a function of study-test congruency may be specific to pictorial information. The transfer-appropriate processing account states that the emphasis on conceptual and perceptual processes at encoding and retrieval and their similarity determines memory success (Roediger et al., 2002). Images are processed with an emphasis on both conceptual and perceptual analysis processes (McBride & Dosher, 2002; Mintzner & Snodgrass, 1995; Nelson et al., 1977). Therefore images are generally processed in a more variable manner than for example words that are processed with a predominant emphasis on conceptual attributes. The emphasis on both perceptual and conceptual attributes might vary as a function of the study-test congruency for stimulus materials such as images. This in turn results in qualitatively different ERP subsequent memory effects.

Therefore, Experiment 3 addressed the question of whether the neural correlates of encoding differ as a function of whether retrieval processes emphasise conceptual or perceptual attributes. In the same vein as previous studies highlighting that encoding-related activity varies depending on the type of encoding strategy (i.e. conceptually driven vs. perceptually driven; Fernandez et al., 1998; Otten & Donchin, 2000; Otten et al., 2007), it was assumed that qualitatively different subsequent memory effects would be evident when the emphasis at retrieval was either on perceptual or conceptual attributes. Pictures were incidentally encoded in a size judgment task. After a short delay, half of the same images were presented again and the other half were presented with a different kind of image that depicted the same object. Retrieval processes were manipulated by using exclusion and inclusion tasks (Jacoby et al., 1993). Participants had to judge whether the presented picture was exactly the same 'picture' as during study or whether the 'concept' depicted by the image was the same as before, irrespective of whether the actual picture was the same. It was suggested that the former task would emphasise perceptual processes and the latter more conceptual processes (cf. Ecker & Zimmer, 2009). Distinct ERP-encoding effects as a function of conceptual and perceptual retrieval processes were not evident in Experiment 3. The experimental parameters such as the trial-by-trial manipulation of both retrieval requirements might have affected the null results. In the previous literature it has been argued that the engagement of specific retrieval orientations refers to a tonically maintained process (Wilding & Rugg, 2000). Therefore, the two different retrieval processes may have been more effectively engaged and maintained across blocks or groups and in turn would lead to qualitatively distinct encoding related ERP effects. Moreover, the findings may highlight the difficulty of isolating conceptual from perceptual processes (cf. Weldon, Roediger & Challis, 1989). The use of images that are free from conceptual content (such as kaleidoscope images, cf. Voss & Paller, 2004) may help to understand encoding-related activity related to perceptual processes in isolation from conceptual processes.

Overall, the three ERP experiments provide good support that encoding-retrieval overlap plays a direct role in long-term memory formation, because study-test congruency effects emerged early after stimulus onset (Cameron et al., 2001). Moreover, because the ERP analyses were restricted to remember responses, the study-test congruency effects may not be confounded by differences in recognition memory types. The findings suggest that encoding-retrieval overlap may play a role for recollection of episodic information. However, it is not clear whether only recollection is sensitive to encoding-retrieval overlap, because know responses were not considered in the ERP analyses. Because study-test congruency was evident only for pictorial information encoding-retrieval overlap may not be a generic organisational principle of the neural correlates of long-term memory encoding.

5.1.2 DOES RETRIEVAL-RELATED BRAIN ACTIVITY VARY WITH THE AMOUNT OF PERCEPTUAL INFORMATION ACROSS ENCODING AND RETRIEVAL?

Experiment 2 addressed whether the perceptually richness at encoding and retrieval affects the neural correlates of recollection. Importantly, the amount of perceptual information modulated retrieval-related ERPs. The study-test congruency manipulation provided the possibility to investigate whether the amount of perceptual information of the encoded content or of the retrieval cue affect retrieval-related ERPs. The findings provide evidence that the amount of perceptual information of the retrieval cue determined the distinct retrieval-related ERP effects. While outlines as test items elicited a left-parietal effect, photographs at test were associated with a more widespread ERP effect. Moreover, photographs showed a significantly smaller left-parietal effect than outlines. This qualitative dissociation was independent of the type of encoded content. The findings indicate that recollection-related ERP effects are sensitive to the amount of perceptual attributes an item contains, because ERP analyses were restricted to remember responses. Moreover, the modulation of old/new effects as a function of perceptually richness emerged within the latency region that is usually associated with recollection (for review see Friedmann & Johnson, 2000). The findings are in line with previous fMRI and ERP findings reporting content-dependent and material-specific recollection-related brain activity (Galli & Otten,

2010; Khader et al. 2005; MacKenzie & Donaldson, 2009; Vaidya et al., 2002; Woodruff et al., 2005; Yick & Wilding, 2008). However, the finding that these effects are specific to the perceptually richness of the test cue does not easily agree with the outlined memory models such as the reinstatement hypothesis or the source framework model that state that the encoded content and its distinct attributes are reinstated which in turn supports the recovery of episodic information (e.g. Mitchell & Johnson, 2009; Norman & O'Reilly, 2003; Rolls, 2000). Moreover, the findings question the interpretation of the left-parietal effect as an index of recollection that refers to the maintenance of episodic information (Vilberg et al., 2008; Wagner et al., 2005, Wilding, 2000). In the discussion section of Chapter 3, it was assumed that the findings may indicate that the processes underlying that effect refer to processes downstream of the recollection of episodic information such as evaluation processes or retrieval monitoring processes (Cruse & Wilding, 2009; Hayama & Rugg, 2008). However, the temporal characteristics of the frontal modulation are inconsistent with the former interpretation. The qualitative dissociation emerged in the time window where recollection-related effects such as the left-parietal effect are expected. The ERP old/new effects related to retrieval monitoring and evaluation processes usually occur in a later latency window after 800 ms (Cruse & Wilding, 2009; Hayama & Rugg, 2008). Thus, the temporal characteristics of the effect suggest that the modulation is directly associated with the recovery of episodic information.

Bearing in mind that recollection refers to reconstruction processes that are based on interactions between the retrieval cue and the memory representation, it may not be surprising that the type of retrieval cue affects the neural correlates of recollection (Tulving, 1983). Outlines as retrieval cues may tap into episodic memory information based on deeper encoded information. If participants successfully recollected episodic information that was cued with an outline, they may have recollected predominantly those items that had been initially encoded with a strong emphasis on deep and semantic processes. In other words, items that were successfully remembered when cued with outlines may have been initially incorporated in more distinct memory representations. The deep or distinct episodic memory traces are in turn associated with larger left-parietal effects for outlines as retrieval cues (Rugg et al., 1998). In contrast, photographs as retrieval cue may access the episodic memory trace easier because these items contain more information and are more familiar (Rugg et al., 1995). In turn, photographs as retrieval cue may have tapped overall into weaker

memory traces or less distinct episodic memory traces which then lead to overall smaller left-parietal effects (Rugg et al., 1995, 1998). However, this interpretation is not in line with the encoding findings in Experiment 2 where encoding-related activity varied with the study-test congruency and not with the type of retrieval cue.

Alternatively, the left-parietal effect may be functionally dissociable from a more anteriorly distributed effect for photographs (cf. Yick & Wilding, 2008). In other words, the anterior contribution may be associated with an additional effect that accompanied the left-parietal effect (cf. Johnson & Rugg, 2008; Yick & Wilding, 2008). The anteriorly distributed modulation may be related to perceptual analysis processes of the retrieval cue that support the recollection of episodic information which is guided by the left-parietal effect. This interpretation is in line with other studies reporting widespread and anteriorly distributed effects for stimulus material that are perceptually rich such as photographs of objects (e.g. Duarte et al., 2004; Galli & Otten, 2010) and faces in comparison to line drawings (e.g. Clearly & Curran, 2003) or words (Galli & Otten , 2010; MacKenzie & Donaldson, 2009; Yick & Wilding, 2008).

This latter interpretation was addressed in Experiment 4. In Experiment 4 the amount of perceptual information was further manipulated to investigate whether retrieval-related brain activity is graded as a function of the amount of perceptual details. Of particular interest was whether retrieval-related differences as a function of the amount of perceptual details are related to differences in retrieval-related ERPs over anterior or parietal sites. Three different images that varied in terms of the amount of perceptual information were presented at study and test: perceptually impoverished outlines, line drawings with an intermediate level of perceptual details and perceptually rich photographs.

Overall memory performance varied depending on the amount of perceptual details. Photographs led to better memory performance than line drawings and outlines. However, memory performance was not graded from outlines to line drawings and photographs. As already outlined in the discussion section in Chapter 3, the mere amendment of perceptual details did not benefit memory retrieval, but possibly the additional information based on other perceptual attributes such as shade or depth information. Interestingly, the retrieval-related ERP effects did not differ depending on the amount of perceptual detail. All three image types elicited widespread old/new effects with left-parietal and right-frontal maxima. The findings did not resemble the material-specific retrieval effects reported in the

previous literature (Galli & Otten, 2010; Mackenzie & Donaldson, 2009; Yick & Wilding, 2008) and in Experiment 2. Various differences in experimental parameters across the experiments were discussed (see discussion in Chapter 3). For instance, Experiment 4 did not manipulate mode of presentation across study and test. The same image type as during study was presented in its mirror-reversed orientation at test. In contrast, the study-test congruency manipulation may have led to a stronger emphasis of perceptual attributes at test in Experiment 2. Thus, the stronger salience of perceptual features may be associated with differences in ERP effects depending on the amount of perceptual details in Experiment 2. In line with this interpretation are the subjective reports of participants in Experiment 2. The participants consistently reported that they noticed the orientation change at test and recollected perceptual changes. In contrast, in Experiment 4 the mode of presentation was not manipulated and participants were not aware about the orientation change at test. Therefore, it was suggested that retrieval-related ERPs may not be influenced per se by the amount of perceptual information, but also by the type of processing focus at retrieval.

Together, Experiment 2 and Experiment 4 showed evidence that the retrieval-related ERPs are not influenced by the mere perceptual match across study and test, but are sensitive to the amount of perceptual information an item contains. Crucially, the retrieval-related ERPs do not vary qualitatively with the encoded amount of perceptual information, but with the perceptually richness of the test probe. It has been demonstrated that the amount of perceptual information may play a direct role in the recovery of episodic information, because the modulation as a function of perceptual information emerged in the latency region when recollection is usually expected. However, the influence of perceptually richness on the neural correlates of recollection may be dependent on other test parameters, such as whether the perceptual attributes are salient at retrieval.

5.1.3 DOES OSCILLATORY THETA POWER ACTIVITY PLAY A ROLE FOR THE REINSTATEMENT OF ENCODING PROCESSES?

In addition to the analysis of event-related potentials, the data of Experiment 2 were analysed in terms of its time-frequency information to investigate whether oscillatory power in the theta frequency domain (4-8Hz) at encoding and retrieval varies depending on the amount of perceptual details of the encoded content or the retrieval cue. Experiment 2 provided the possibility to investigate the effects of neural reinstatement. The time-frequency analysis for both encoding and retrieval was expected to elucidate whether theta oscillatory power varies as a function of encoding-retrieval overlap.

Photographs were associated with an encoding-related theta power increase over left frontal locations, regardless of the type of test probe. In contrast, encoded outlines did not show encoding-related theta increases. At retrieval, again a retrieval-related theta power increase over frontal locations was evident for encoded photographs, irrespective of the type of retrieval cue. Outlines elicited theta power increases only over left-parietal locations. These findings indicate that frontal theta at both encoding and retrieval depends on the amount of perceptual information contained within an encoded event. The findings may suggest that frontal theta power increase plays a role for the reinstatement of encoded context.

Because frontal theta power increase was selectively evident for encoded photographs at encoding and retrieval, the findings are in line with neurocomputational models that suggest that frontal theta oscillations may play an important role for the reinstatement of memory representations leading to the recovery of episodic information (cf. Nyhus & Curran, 2010; Polyn & Kahana, 2008; Rolls, 2000). The findings are consistent with studies demonstrating that theta power increase over frontal sites is associated with the recollection of specific details of the studied episode (Addante et al., 2011; Gruber et al., 2008; Guderian & Düzel, 2005). Based on neurocomputational models (e.g. Polyn & Kahana, 2008) it is expected that theta oscillations support dynamic interactions between prefrontal cortex, hippocampus and the posterior cortex (cf. Guderian & Düzel, 2005). However, it is unlikely that oscillations generated from deeper structures such as the hippocampus are evident in the EEG. Future studies using methods that have a higher spatial

resolution such as MEG or iEEG need to pinpoint the underlying brain regions that are related to the oscillatory activity presented in Chapter 4.

Crucially, study-test congruency of mode of presentation did not modulate theta power increases at encoding and retrieval. According to the transfer-appropriate framework one would have suggested more neural reinstatement for a perceptual match, because memory benefited from an overlap between encoding and retrieval operations. Maybe oscillatory activity in other frequency bands such as gamma (> 25 Hz) that is associated with feature binding (Hoogenboom, Schoffelen, Oostenveld, Parkes & Fries, 2006) may be sensitive to the physical similarity between study and test mode of presentation.

What is the functional significance of a frontal and a left-parietal retrieval-related theta-power increase? If a frontal-theta power increase at encoding and retrieval is related to the reinstatement of photographs, it is not clear why outlines do not show reinstatement effects, because memory performance did not differ between outlines and photographs. Because of the relatively early occurrence of the frontal theta effect (~400 ms) it is unlikely that the underlying processes are downstream of recollection processes such as retrieval monitoring processes (Wilding & Rugg, 2000). Therefore, it was assumed that the retrieval-related theta power increase is directly associated with the recollection of episodic details. Previous studies associated oscillatory activity in the theta frequency band (4-8Hz) to top-down control processes supporting episodic encoding and retrieval (for reviews see Nyhus & Curran, 2010; Klimesch et al., 2008; Burgess & Gruzelier, 1997; Klimesch et al., 1996; Sederberg et al., 2007; Summerfield & Mangels, 2005). Therefore, perceptually rich photographs may have engaged more control processes during encoding, because more information had to be incorporated into new memory representations. In the same vein, more control processes may have been engaged at retrieval to recover rich perceptual information when studied photographs are retrieved.

A left-parietal theta-increase was evident for both outlines and photographs at retrieval. A left-parietal theta power increase has been associated with left-parietal ERP old/new effects in the previous literature (e.g. Addante et al., 2011; Klimesch et al., 2001). The left-parietal ERP effect has been associated with generic recollection processes are thought to be content-independent and material-unspecific (Rugg et al., 1998). Therefore, it may be possible that the parietal theta power increase guides general recollection processes for outlines and photographs. The additional frontal contribution for encoded photographs may be specific to the recollection of the amount of perceptual information that needs to be recovered.

In accordance with the ERP findings of Experiment 2, time-frequency information showed no study-test congruency effect at retrieval. However, in contrast to the ERP results, the time-frequency results did not show study-test congruency effects at encoding. Both encoding-and retrieval-related oscillatory theta power increases were solely influenced by the encoded image type and not by the amount of perceptual information of the retrieval cue. Thus, the time frequency findings may reflect different underlying processes as the ERP findings in Experiment 2. Although ERP and time-frequency analysis approaches are based on the same data, they do not necessarily tap into the same kind of processes. Instead they may contain complementary information about the underlying cognitive functions. Previous research has demonstrated that ERPs and oscillatory activity can reflect similar processes such as early attention-specific ERP effects (i.e. P1 and N1) that are suggested to refer to phase synchrony of alpha and theta oscillatory activity (Makeig et al., 2002). However, little is known about whether slow-wave potentials such as in the current experiments directly map onto oscillatory activities. The time-frequency data contain different types of information such as induced responses that are usually cancelled out with the ERP approach (Bastiaansen et al., 2008). For instance, Klimesch (1999) showed that the neural generators of activity patterns related to recognition memory can differ as a function of whether the activity refers to induced oscillations or ERPs (cf. Düzel et al., 2005). In contrast to the ERP approach, analysing electrophysiological activity in terms of its time-frequency information provides the opportunity to directly investigate, similarly to fMRI, the neural overlap between encoding and retrieval. While methodologically a comparison between encoding-related and retrieval-related ERP effects is as yet difficult, the investigation of oscillatory activity in a specific frequency range provides the possibility to compare both types of neural correlates.

Interestingly, a recent study demonstrated frontal theta power increase at retrieval already before the retrieval cue onset. This was specific to the successful recollection of specific encoded details. The effect correlated positively with memory performance. The authors suggested that frontal theta power increase before the retrieval cue is associated with the reinstatement of the encoded context which in turn supports later recollection (Addante et al., 2011). This highlights the possibility that oscillatory activity in the theta frequency band sets already a specific contextual state before the retrieval cue is processed that supports later recollection. Moreover, consistent with the neural reinstatement of encoding processes for recognition based memories, a recent study (Manning, Polyn, Baltuch, Litt & Kahana, 2011) found evidence for context reinstatement of oscillatory activity patterns in free recall tests. Manning et al. (2011) analysed electrocorticographic recordings and demonstrated that the oscillatory activity during successful free recall was not only similar to the activity patterns during encoding, but also to the activity of the neighbouring items during the study phase. Furthermore, the neural reinstatement effect correlated with the recall performance of the neighbouring items. Therefore, the neural reinstatement of the studied context is also evident for free recall of encoded information.

Together, the time-frequency analyses at encoding and retrieval provide evidence for the neural reinstatement models and may suggest that frontal oscillatory theta activity plays an important role in the reinstatement of encoded content. The early occurrence of frontally distributed theta-power increases at encoding and retrieval indicate that neural reinstatements of encoding processes are directly related to recollection rather than a consequence.

5.2 IMPLICATIONS AND FUTURE RESEARCH

My PhD research provided evidence that an overlap in encoding and retrieval processes affects the neural correlates of long-term memory. The findings demonstrated that particularly encoding-related activity was modulated by the study-test congruency of mode of presentation and the type of retrieval process (cf. Bridger & Wilding, 2010; Otten, 2007; Park & Rugg, 2008; Wimber et al., 2010). This has important implications for the interpretation and comparison of memory-related brain activity across populations, such as elderly or patient groups. For instance, a significant difference in the neural correlates of encoding between young and elderly participants may not refer to deficits in encoding processes. Differences in retrieval strategies and the interplay between encoding and retrieval processes across groups may have affected the different activity patterns at encoding (cf. Otten, 2007). These effects in turn may vary depending on which type of information and stimulus category has been encountered. Thus, interpretations of neuroimaging findings need to consider cautiously differences in encoding processes, retrieval processes and the overlap between both processes.

My PhD research also demonstrated that the overlap between encoding and retrieval operations may not under all circumstances play a role in the neural correlates of long-term memory. Thus, encoding-retrieval overlap may not be a universal organisational principle of the neural correlates of memory. Encoding-retrieval overlap effects depend on the type of information contained within an encoded event and retrieval cue, and the type of neural activity that is considered.

Experiment 3 showed that a differentiation in either perceptual or conceptual processes as a basis for the encoding-retrieval overlap effect may be more difficult than originally suggested (c.f. Weldon et al., 1998). The application of neuroscientific methods with higher spatial resolution such as fMRI may help to gain a full understanding of the functional processes related to encoding-related study-test congruency effects. Although the temporal resolution is low, the high spatial resolution of fMRI may help to pinpoint the neural generators of the processes related to conceptual and perceptual processes and the similarity across encoding and retrieval. Interestingly, a recent fMRI study (Wimber et al., 2010) reported encoding-related activations of specific brain regions as a function of whether the

memory test was perceptually driven or conceptually driven. During encoding the ventral posterior parietal and dorsolateral prefrontal cortex was associated with words that were correctly recognised in a perceptual identification task (perceptually driven). In contrast, these encoded words that were correctly recognised in the recognition test (conceptually driven) showed activation of ventrolateral prefrontal and dorsal posterior parietal cortex. Based on those findings, the authors suggested that ventral parietal regions may play an important role for the successful encoding of perceptual attributes, while dorsal parietal regions were associated with encoding processes of conceptual attributes of the event. However, in addition to the different types of processes that are emphasised in both tests (perceptual versus conceptual), both memory tests may tap into different types of memory systems (i.e. implicit vs. explicit memory; Tulving, 1983). Moreover, it is not clear if the combined perceptual identification test and standard recognition test affects encoding-related activity in a similar way than a standard recognition test in absence of the perceptual identification task. In the same vein as in Wimber et al. (2010), one could pinpoint the loci in the brain which are affected by the study-test overlap through a neuroscientific method that is high in spatial resolution such as fMRI. In combination with the subsequent memory analysis, it is possible to compare neural activity according to the different encoding and retrieval conditions (e.g. study-test match; study-test mismatch).
If the interpretation of the encoding findings in Experiments 1 and 2 holds to be true, similar dissociations in encoding-related activations may be evident as in Wimber et al. (2010) as a function of whether images were cued in the congruent mode of presentation or incongruent mode of presentation. For instance, if the posterior subsequent memory effect for the picture-word condition is indeed related to perceptual processes, then it may be expected that similar brain regions would be engaged as in the perceptual identification task in Wimber et al (2010). The same would be suggested when cueing later memory with a picture instruction in Experiment 3, where participants only accept items as old if they were indentical to the ones presented at study.

5.2.1 FUTURE DIRECTIONS: INVESTIGATING THE NEURAL CORRELATES OF RETRIEVAL

In my PhD research, the retrieval-related ERPs differed qualitatively depending on the amount of perceptually richness the retrieval cue contained. It is yet not clear why recollection-related effects show retrieval cue specific effects. At first glance, these modulations are inconsistent with the well-established interpretation of the left-parietal effect that is thought to be an index of recollection and refers to the maintenance of memory representations (Vilberg et al., 2008; Wagner et al., 2005; Wilding, 2000). Further research needs to be conducted to replicate the test probe-specific modulations of recollection-related effects in Experiment 2 and elucidate the underlying functional significance. For instance, instead of manipulating the amount of perceptual information an item contains, the encoded information or context could be manipulated in terms of whether the encoding strategy emphasises a great number or small number of perceptual information by keeping the stimulus identical. Source memory tests could be applied to explicitly highlight the recollection of the perceptual information. Source memory refers to the recollection of specific features (e.g. colour of object) of the studied episode. However, source memory tests are not free from criticism. An incorrect source judgement does not necessarily mean an absence of recollection, because other details of the studied episode than the one specified in the source memory test may have been remembered (e.g. Vilberg & Rugg, 2008).

Moreover, to generalise that frontal recollection-related contributions refer to the amount of perceptually richness an item contains it may be of importance to vary the amount of perceptual information in different stimulus categories such as faces that have also been associated with more frontal contributions in the previous literature (e.g. MacKenzie & Donaldson, 2009; Yick & Wilding, 2008). In a future study, a similar design as in Experiment 2 could be applied to faces. It would be expected that both outlines of objects and faces are associated with a left-parietal effect, while stimuli containing rich perceptual information of faces and photographs elicit a widespread recollection-related effect.

5.2.2 FUTURE DIRECTIONS: RELEVANCE OF ENCODING-RETRIEVAL OVERLAP FOR DIFFERENT TYPES OF RECOGNITION MEMORIES

The ERP and time-frequency analyses were restricted to remember responses to elucidate how encoding-retrieval overlap affects the neural correlates of long-term memory based on recollection or strong memories. The low number of trials of 'know' responses and corresponding low signal-to-noise ratio made it impossible to analyse this category in isolation. The analyses restricted to remember responses may indicate that encoding-retrieval overlap plays a role for recollection based memories. However, because the brain activity related to know responses was not considered, one cannot conclude that encoding-retrieval overlap plays a selective role in recollection which is predicted by the neural models of episodic memory (e.g. Norman & O'Reilly, 2003).

Future studies need to highlight whether neural correlates based on familiarity-related judgements show similar study-test congruency effects or differ qualitatively from recollection-related effects. Previous studies investigating the neural bases of encoding-retrieval overlap on recognition memory only considered old/new judgments (e.g. Park & Rugg, 2008; Schloerscheidt & Rugg, 2004). However, a recent event-related fMRI study (Otten, 2007) demonstrated that encoding activity predicting successful recognition based on familiarity was associated with distinct brain regions relative to recollection-related brain regions as a function of the type of retrieval cue. In line with the neuroimaging findings, behavioural findings that aimed to dissociate between the different types of recognition memory demonstrate inconsistent results as of whether encoding-retrieval overlap selectively affects recollection or familiarity. While some studies demonstrate that perceptual congruency only affects recollection (Reder et al., 2002; Hirshman et al., 1999), other studies show study-test congruency effects specific to familiarity (Jacoby, 1996), and for both recollection and familiarity (Rajaram, 1993). Future studies, therefore, need to elucidate whether study-test congruency affects recollection, familiarity, or both.

5.2.3 FUTURE DIRECTIONS: OSCILLATORY BRAIN ACTIVITY AND ENCODING-RETRIEVAL OVERLAP

Chapter 4 outlined the attempt to investigate whether encoding-retrieval overlap and the amount of perceptual details modulates oscillatory power in the theta frequency band. The findings show good evidence that theta oscillations play a role in the neural overlap between encoding and retrieval. It would be of interest to elucidate whether the reinstatement of encoding processes evident in Chapter 4 is selective for recollection of episodic information as it is proposed in neural models of episodic memory (Norman & O'Reilly, 2003). Recollection has been selectively associated with the reinstatement of episodic information, because the hippocampus refers to the core region where memory representations are stored and which induces cortical reactivation. However, a recent fMRI study (Johnson et al., 2009) has demonstrated that reinstatement of encoding processes is not specific to recollection, but also affects familiarity-based responses. Therefore, further studies need to address similar research questions to elucidate whether the reinstatement of encoded processes is indeed the driving factor supporting recollection (Johnson et al., 2009).

In addition, it is of importance to elucidate whether oscillatory activity within other frequency bands plays a role in encoding-retrieval overlap. For instance, gamma oscillations (> 25 Hz) are also thought to play an important role in memory functions (for reviews see Düzel et al., 2010; Nyhus & Curran, 2010; Klimesch et al., 2008). Similar functions as for theta oscillations are associated with gamma rhythms regarding dynamic connections between the hippocampus and cortical areas at encoding and retrieval to support the cortical reinstatement of memory representations. Particularly, encoding-related gamma power increase was demonstrated in the hippocampus and the posterior cortex (Gruber et al., 2008; Hanslmayr et al., 2009; Osipova et al., 2006; Summerfield & Mangels, 2005). Such gamma synchronization is thought to support the binding of specific stimulus features such as perceptual attributes and other contextual details from different brain areas into coherent memory representations (Nyhus & Curran, 2010). For instance, previous research showed evidence that encoding-related oscillatory gamma power was associated with modality-specific and visual brain regions (for review see Nyhus & Curran, 2010). Interestingly, gamma oscillations have been associated with feature binding (Hoogertsboom et al., 2006) and matching mechanisms between stimulus

features and the memory representations (Hermann et al., 2005). Therefore, it would be expected that particularly gamma oscillations may be sensitive to the study-test congruency of the mode of presentation. Oscillatory activity in the gamma frequency band may dissociate between early perceptual modulations and later memory formation processes.

In addition, of particular interest would be to discern how the inter-trial coherence of oscillatory phases or phase-locking respectively is influenced by encoding-retrieval overlap (for review see Sauseng & Klimesch, 2008). The oscillatory phase can reflect fast and dynamic interactions between neural populations that are functionally related (Sauseng & Klimesch, 2008). The phase synchronization or coupling respectively between theta and gamma frequencies is thought to play an important role in episodic memory functions (Düzel et al., 2010; Lisman & Busaki, 2008; Nyhus & Curran, 2010). Particularly, encoding-related functioning is thought to depend on the dynamic interactions of gamma and theta (Fell & Axmacher, 2011). It has been suggested that gamma refers to the processing of the incoming sensory information and theta supports the integration of this information into coherent memory representations (Fell et al., 2001; Lisman & Buzsaki, 2008). Therefore, more insights about the dynamic brain networks and the role of encoding-retrieval overlap would be gained by studying other frequency bands and importantly the interaction between different frequency bands.

Recent analysis methods such as multi-pattern analysis in combination with an acquisition method that has a higher spatial resolution such as MEG will help to draw more direct conclusions about the neural overlap between encoding and retrieval and the encoded content. These methods are assumed to be more sensitive to detect reinstatement (Johnson et al., 2009; Norman et al., 2006). For instance, a recent MEG study applied successfully multi-pattern classifiers to the maintenance phase of a working memory paradigm. Specific activity patterns in the theta frequency band were identified as a function of the perceptual attributes of the encoded item (indoor, outdoor scene) and the encoding focus (i.e. on associations between scene features vs. single features) (Fuentemilla et al., 2010). Moreover, oscillatory theta activity was correlated with the working memory performance. In the same vein, pattern classifiers could be trained with encoding-related brain activity to identify activity patterns specific to the encoded content within the retrieval-related activity in a long-term memory recognition paradigm like the one used in my PhD studies. For

instance, in Experiment 2 it would be expected, in accordance with the neural models of episodic memory (e.g. Norman & O'Reilly, 2003), that specific encoding-related oscillatory activity patterns in the theta frequency band can be identified at retrieval. Thus, the combination of multivariate pattern classifiers and MEG which has a good temporal resolution and spatial resolution, may elucidate the underlying brain regions associated with theta oscillatory activity that are related to encoding-retrieval overlap.

Interestingly, there are recent EEG and MEG studies that combine the research in the field of brain oscillations and the research using repetitive (i.e. rhythmic) transcranial stimulation (TMS) to gain more insights about the functional role of brain oscillations and how to apply this to the therapeutic and clinical settings (for review see Huerta & Volpe, 2009; Thut & Miniussi, 2009, 2010). The combination of both techniques is thought to provide complementary information about the correlational and causal relationship between brain activity and cognitions (Miniussi & Thut, 2010). Recent studies using rhythmic TMS showed evidence that specific cognitive functions can be modulated by inducing rhythmic TMS (for review see Mimiussi & Thut, 2010). For instance, Klimesch, Sauseng and Gerloff (2003) demonstrated that rhythmic TMS stimulation of frontal and parietal locations selectively in the alpha frequency band affected performance in a visual spatial task (cf. Thut & Miniussi, 2009). Moreover, Marshall, Kirov, Brade, Mölle and Born (2011) demonstrated that transcranial direct current stimulation (tDCS) at 5 Hz within the theta-frequency range increased selectively gamma (25-45 Hz) activity during REM sleep which affected memory consolidation. Moreover, a recent study that applied transcranial slow oscillation stimulation (0.75 Hz) was associated with increased theta activity and improved memory encoding (Kirov, Weiss, Siebner, Born & Marshall, 2009). Based on the findings in the present study and previous research, it would be of interest to elucidate how transcranical brain stimulation within the theta frequency range over frontal sites at encoding and retrieval affects task performance in a later recognition memory test. Moreover, selective stimulations at encoding may elucidate a direct role of theta in reinstatement processes. The induced oscillations are expected to be reinstated at retrieval which in turn leads to successful memory retrieval. Together, the combination of EEG and TMS may help to elucidate how brain oscillations are related to specific brain functions across encoding and retrieval.

Furthermore, recent studies demonstrated that the inducing of oscillations within a specific frequency range via neurofeedback training could improve cognitive functioning (Dohrmann, Weisz, Schlee, Hartmann & Elbert, 2007). For instance, the enhancement of alpha oscillations via neurofeedback training diminished uncomfortable auditory sensations of tinnitus patients (cf. Tuth & Miniussi, 2009; Dohrmann et al., 2007; van Gerven & Jensen, 2009). This potentially opens a new horizon for treatments of other cognitive dysfunctions such as memory deficits in elderly or patient populations. For example, within the context of my PhD experiment it may be possible to train participants to induce oscillations within the similar frequency range at study and test such as an increase in frontal theta oscillations at encoding and at retrieval which in turn may result into an improvement of memory performance.

5.3 FINAL CONCLUSION

My PhD studies aimed to elucidate how the interplay between encoding and retrieval affects electrical brain activity of human long-term memory. Four EEG studies were conducted to address this main research question. I demonstrated that the interaction between encoding and retrieval processes plays a relevant role in human long-term memory. However, study-test overlap may not be a universal organizing principle of the neural correlates of long-term memory. The influence of study-test congruency depends on the specific attributes the stimulus consists of at both encoding and retrieval and on the specific type of neural activity.

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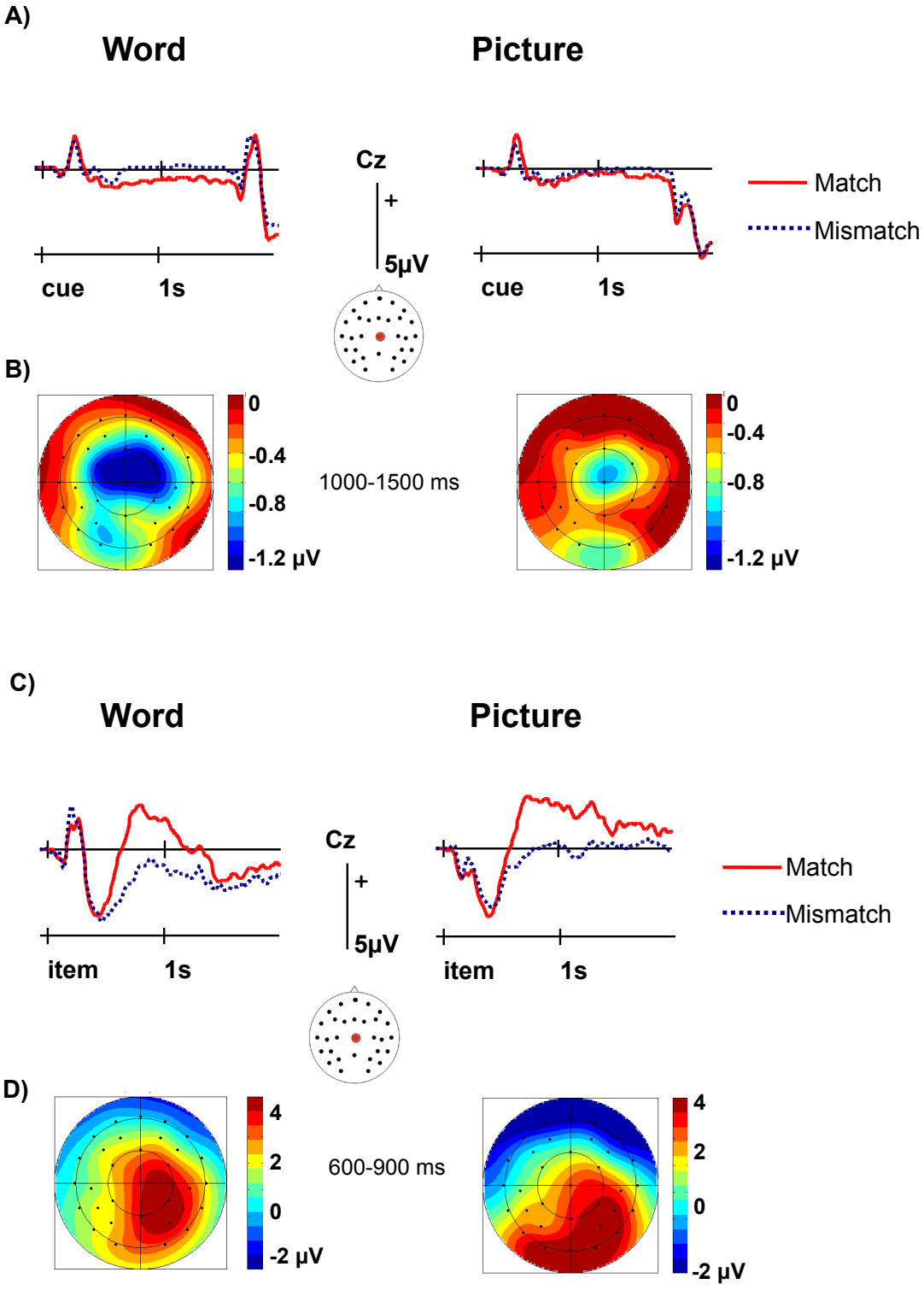
7. APPENDICES

7.1 APPENDIX 1



Appendix 1.1. A) Retrieval orientation activity in Experiment 1 associated with the letter cue 'W' and 'P'. Group averaged ERP waveforms at test are compared for the Match group (solid line) versus Mismatch group (dotted line) for the 'W' cue (left) and 'P' cue (right). The waveforms of one electrode site (equivalent to Cz of the international 10/10 system) is displayed. Whereas ERPs elicited by cues that signalled an upcoming word ('W') were more negative-going in the Match than Mismatch group over central scalp sites 500 ms before item onset, ERPs between groups did not differ for cues signalling upcoming pictures ('P'). Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes. B) The spline maps illustrate the scalp distribution of the difference activity between Match and Mismatch groups for the 'W' and 'P' cues in the latency region of 600-900 ms. C) Retrieval orientation activity associated with the test item. Group averaged ERP waveforms at test of correct new responses are compared for the Match group (solid line) versus the Mismatch group (dotted line) for words (left) and pictures (right). The waveforms of one electrode site (equivalent to Cz of the international 10/10 system) is shown. ERPs elicited by new words and pictures were both more positive-going in the Match than Mismatch groups. D) The scalp distribution of this 'retrieval orientation' effect was more posterior for pictures than words. This effect across words and pictures changed its polarity over anterior locations.

Appendix 1.2. F statistics and *p* values of the key effects in the across-goup ANOVA on the retrieval activity associated with the letter cues. The statistics confirm the observations. Whereas activity associated with 'P' cues did not differ between the Match group and Mismatch group, retrieval-related brain activity varied significantly between both groups for 'W' cues (significant main effect of group).

Cue type		1000 – 1500 ms
	GP x IT	$F(1,46) = 4.83, p = .033$
'W' cue	GP	$F(1,46) = 8.88, p = .005$
'P' cue	GP	$F(1,46) = 1.29, p = .264$

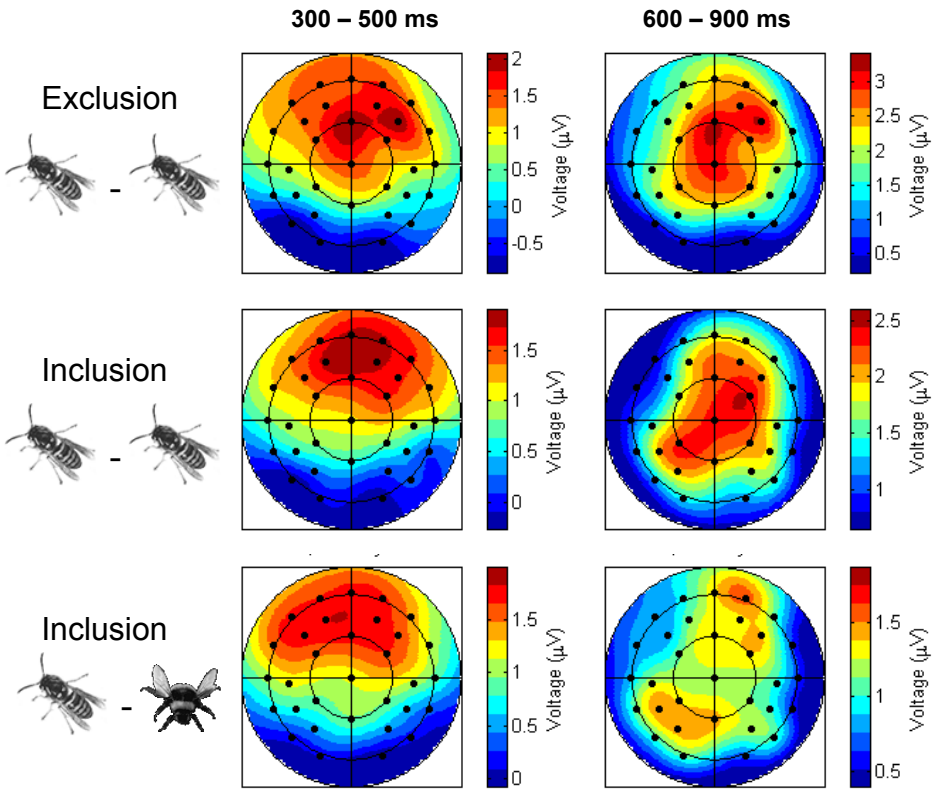
GP = group; IT = cue type

Appendix 1.3. F statistics and *p* values of the key effects in the across-goup ANOVA on the retrieval activity associated with the new test items. The statistics confirm the observations. The ERPs associated with the Match and Mismatch group differed significantly across the scalp as a function of the item type (picture/word).

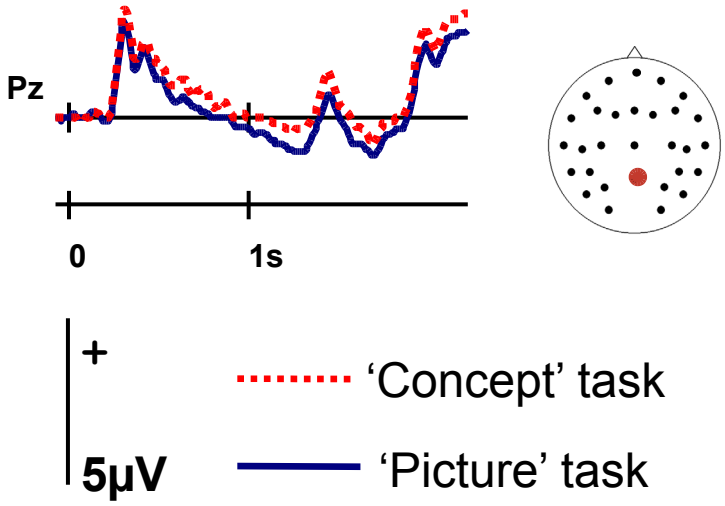
Item type		600 – 900 ms
GP x IT x ST		$F(3.5,162.4) = 4.04, p = .005$
Words	GP	$F(1,46) = 15.25, p < .0001$
Pictures	GP x ST	$F(2.6,120.5) = 6.26, p = .001$

Degrees of freedom and *p* values are Greenhouse-Geisser corrected, GP = group; IT = Item type; ST = electrode site

7.2 APPENDIX 2



Appendix 2.1. The spline maps illustrate the scalp distribution of the difference in activity at retrieval in Experiment 3 between confident old and correct new responses for the copy cues in the 'Picture' task and'Concept' task and for exemplars in the'Concept' condition in the latency regions of 300-500 ms and 600-900 ms. All three conditions showed an old/new effect over midfrontal locations in the early time region and a widespread old/new effect in the later latency region (see Appendix 2.3 for statistics).



Appendix 2.2. Group averaged ERP waveforms associated with the verbal cues signaling the upcoming task at test. The retrieval orientation activity is collapsed across responses (old and new) and item types (exemplar and copy cue). ERP waveforms are compared across the 'Concept' (red) and 'Picture' (blue) tasks (Ecker & Zimmer, 2009). The waveforms of one electrode site (equivalent to Cz of the international 10/10 system) is displayed. Positive values are plotted upwards. The waveforms are high frequency filtered with a cut-off point of 15.5 Hz for display purposes. Group averaged ERPs did not differ as a function of the type of retrieval task (p = .188).

Appendix 2.3. F statistics and *p* values of the key effects retrieval success data in Experiment 3. Old/new effects (confident old minus correct new) did not differ qualitatively between the three retrieval condition in an early latency region that is usually associated with familiarity-related recognition and within a later latency region that has been associated with recollection-based recognition,

Task			300-500 ms		900-1300 ms
		TAxONxST	$F(6.1,140.6) = .586$, $p = .743$		$F(4.8,109.3) = 1.88$, $p = .108$
'Picture'	Old identical	ONxST	$F(3.5,81.0) = 11.28$, $p < .0001$	ONxST	$F(3.5,80.5) = 4.135$, $p = .006$
'Concept'	Old identical	ONxST	$F(3.4,77.2) = 5.62$, $p = .001$	ONxST	$F(3.6,83.8) = 3.85$, $p = .008$
	Old exemplar	ONxST	$F(3.0,69.5) = 5.81$, $p = .001$	ON	$F(1,23) = 11.56$, $p = .002$

Degrees of freedom and *p* values are Greenhouse-Geisser corrected. TA = retrieval condition; ON = old/new; ST = electrode site